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Psychological Review

EDITED BY
HERBERT S. LANGFELD
PRINCETON UNIVERSITY

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THE PSYCHOLOGICAL REVIEW

SYMPOSIUM ON HEREDITY AND ENVIRONMENT[1]

EVOLUTIONARY CHANGES IN THE PHYSIOLOGICAL CONTROL OF MATING BEHAVIOR IN MAMMALS

BY FRANK A. BEACH

Department of Psychology, Yale University

INTRODUCTION

In agreeing to discuss any aspect of the so-called 'heredity-environment' problem one naturally infers that the artificiality of the implied dichotomy is obvious to everyone. It has long been apparent that a strict separation of the effects of inheritance from those of the individual's environment is impossible from a practical point of view and undesirable from a theoretical one. However, the basic problem can be re-formulated in a way that will permit its systematic exploration.

Every behavioral act constitutes a response to external and internal stimuli. In order to evoke overt reactions the stimuli must be transformed into nervous energy which is transmitted from peripheral receptors to various integrative mechanisms of the central nervous system; and these mechanisms in turn excite others whose activity elicits the muscular or glandular changes that constitute the behavior which we observe. It is abundantly clear that the structural organization of the neuromuscular constitution is determined primarily by the action of genic forces, and there is ample reason to believe that many functional characteristics of this same system are equally dependent upon genetic control. On the other hand the functional capacities and responsiveness of certain parts of the nervous system are quite labile and may undergo marked alteration as a result of previous excitations. In effect this means that when mechanisms of the latter type are involved the behavior which will be elicited by a given set of stimuli depends to a large extent upon the previous experience of the individual.

Employing this general type of formulation, we can state the heredity-environment problem as it affects a particular pattern of behavior in the following interrogative form: To what extent are the occurrence and nature of a given behavioral response governed by genetically-determined structuro-functional characteristics of the neuromuscular constitution, and to what degree are the appearance and form

[1] This issue is devoted to the publication of a Symposium on Heredity and Environment presented at the annual meeting of the Society of Experimental Psychologists on April 10, 1947 at Princeton University in connection with the Bicentennial Celebration.

of the response due to modifications brought about in this constitution by experience?

We need not be overly concerned if at this point some purist arises to protest that the very lability of particular nervous mechanisms is a function of genetic constitution, and that the most 'stereotyped' neuromuscular relationships may be modified through exercise. Such criticisms may be true enough but it is not necessary that we allow ourselves to be pushed into an extreme position, for few would deny that *relative* differences in modifiability do exist; and it is with such differences that we shall deal in the following discussion.

It is our purpose to review briefly experimental evidence concerning the physiological basis for sexual arousal and mating behavior in various mammalian species with a view to estimating the relative importance of heredity and environment at different levels of the phylogenetic scale; and in this case the term 'environment' is taken to mean specifically the effects of experience.

ENDOCRINOLOGICAL EVIDENCE

Like any other pattern of response sexual activity consists of a series of overt reactions to external stimuli; but unlike many other types of behavior the courtship and mating of most mammalian species depend heavily and specifically upon secretory products of certain endocrine glands. It is to the importance of the hormones that we shall first turn our attention.

Hormonal factors in the sexual behavior of the female

Evidence attesting the importance of ovarian hormones to sexual receptivity in female mammals comes from several sources.

Behavioral changes accompanying puberty. Sexually immature female rodents, lagomorphs and carnivores show none of the separate responses which characterize the behavior of the adult female in estrus. The juvenile rat, rabbit or cat apparently does not represent a sexually-exciting object to the reproductively mature male, and when the prepubescent female is subjected to exteroceptive stimuli adequate to elicit heat reactions in the full-grown individual, the adult pattern fails to appear. At puberty, when the ovary becomes active and mature follicles develop, the initial estrous period occurs and the mature mating pattern appears full blown. It is at this time that the concentration of ovarian hormones abruptly increases, and the observed correlation has been taken as presumptive evidence for a causal relationship.

Supporting evidence for this assumption is to be found in reports of the experimental induction of precocious puberty in females of several lower mammalian species. The quiescent ovaries of immature rats (33) and mice (94) respond to administration of gonadotrophic (gonad-stimulating) hormones with follicular growth and consequent secretion of ovarian hormones. When this occurs the young animals display all of the elements of the adult female's mating pattern. Identical results are obtained if the pituitary is by-passed and the prepubescent female is treated with ovarian hormones (14, 68). Findings of this nature indicate two important conclusions. First, the ovary is capable of responding to stimulation by pituitary hormones well in advance of the time that such hormones normally become available; and second, the neuromuscular mechanisms responsible for heat behavior are fully organized and susceptible to sensitization by ovarian hormones long before the latter are secreted.

The second point has interesting implications, for if one could find a species in which ovarian hormones were

not essential to activation of the neuromuscular mechanisms mediating feminine sexual responses, it might be expected that such responses would appear prior to the puberal increase in gonadal secretions. As a matter of fact such a situation appears to obtain in the case of the anthropoids, for very young female chimpanzees do exhibit sexual behavior years before the ovarian cycle is initiated. Observations of the play of infant apes have revealed the frequent occurrence of copulatory responses which develop as far as intromission and pelvic movements (24). Comparable behavior occurs in human children in free social situations. Although the sexual play of children in Western cultures is severely restricted (82, 89), it is well known that under less rigorous repression young boys and girls will indulge in coital mimicry involving nearly all of the elements of adult copulatory performance (73).

Behavioral changes accompanying ovarian cycles. The mating activity of most mammalian species is sharply retricted to a brief period of the year, at which time the reproductive organs of both sexes become hypertrophied and the level of gonadal hormones rises abruptly (100). Females of such seasonally breeding forms display sexual receptivity when the ovaries contain large follicles and the concentration of ovarian hormones is high (56, 57). The belief that heat behavior results directly from the altered hormonal balance receives support from numerous experiments in which estrus has been artificially induced outside of the normal season by the administration of pituitary or ovarian hormones (34, 51, 53, 57, 58, 118).

Females of polyestrous species come into heat at regular intervals throughout all or most of the year. The rat, for example, is in estrus once every four to five days unless pregnancy intervenes. A variety of experiments involving the suppression of normal cycles or the stimulation of artificial ones have provided proof that the behavioral characteristics of estrus are dependent upon high levels of ovarian hormones (45, 114).

Although a close relationship between ovarian condition and sexual receptivity appears to be the rule in subprimate mammals, the situation is somewhat different in higher forms. There is little evidence on this point as far as the more primitive primates are concerned (70), but in the case of both New and Old World monkeys there are indications that copulation is not entirely restricted to the female's fertile period. It should be understood that the hormonal events of the ovarian cycle are just as clear-cut in one mammalian species as in another, and the reproductive rhythm of the female monkey, ape or human is nearly as regular and invariable as that of the rat. Therefore the fact that the female rhesus will occasionally permit copulation by the male at times when her ovaries are inactive indicates a slight degree of emancipation from the hormonal control of such behavior (28, 29).

A much higher degree of freedom is evident in the sexual life of the female ape. Chimpanzees exhibit a well defined rhythm of ovarian activity, and parallel to the increase and decrease in sex hormones there occur periodic fluctuations in eagerness for sexual contact. However, it is well known that non-hormonal factors exert a strong influence upon chimpanzee sexuality, and under a variety of social situations complete mating may occur at any stage in the female's reproductive cycle (108, 115, 116).

The existence of variations in sex desire correlated with stages of the menstrual cycle of the human female has

been debated at length (38, 41, 104); however, the important point for the present discussion would seem to be not whether such a cycle does or does not exist, but that in our own species the potential effects of ovarian hormones are so obscure as to be nearly if not entirely unrecognizable.

Behavioral effects of ovariectomy. The foregoing evidence makes it apparent that the dependence of sexual activity upon ovarian hormones is very strong in lower mammals, somewhat less pronounced in monkeys, decidedly reduced in apes and least obvious of all in the human female. Studies of the effects of removal of the ovaries and experimental replacement of ovarian hormones have yielded results in harmony with this generalization.

Ovariectomy of prepuberal rats, guinea pigs, rabbits, and other lower mammals precludes the occurrence of mating responses in adulthood (117), and similar operation after the attainment of reproductive maturity promptly and permanently abolishes all manifestations of sexual heat in rodents (60, 103, 112), ungulates (3, 78) and carnivores (8, 66, 68, 71). Regardless of the age at operation, it is possible to bring out normal coital responses in the ovariectomized female during adulthood by the injection of the appropriate ovarian hormones. This has been found true in the case of the guinea pig (25), hamster (49), mouse (84), rat (16), dog (66), cat (8), ferret (76), sheep (78) and cow (1). The only published study dealing with subanthropoid primates indicates that although the female rhesus monkey refuses the male after loss of the gonads, she will become sexually receptive if estrogen is injected.

Female chimpanzees, in contrast, sometimes exhibit sexual receptivity despite loss of the sex glands, although such behavior is said to occur infrequently and to be submaximal in intensity. Spayed apes receiving estrogen show swelling of the sex skin and receive the male in a manner indistinguishable from that of the intact female during the fertile period (32).

The psychological sequelae to ovariectomy in the human female are highly variable but there is little question that sexual desire and capacity are unchanged in a high proportion of the women so operated (47, 74, 109). Similarly the effects of menopausal change show marked individual differences, and in many women the desire for and enjoyment of sexual contact continues undiminished. The effects of estrogen therapy are ambiguous. A few women who have suffered loss of libido as a result of ovarian regression or removal report the restoration of sexual interests under hormonal therapy, but other patients who suffer diminished responsiveness consequent to gonadal loss experience no relief when exogenous estrogen is supplied (54, 59).

Evidence pertaining to prepuberal sexual activity, to the correlation of sexual behavior with cycles of ovarian secretion and to the effects of ovariectomy followed by replacement therapy suggests that advancing phyletic status is accompanied by progressive relaxation of rigorous hormonal control over sexual receptivity. It appears that in the course of mammalian evolution, and specifically in the development of the primate stem, the physiological basis for sexual behavior has undergone certain modifications which have tended to free the female's sexual responsiveness from complete dependence upon ovarian hormones.

Hormonal factors in the sexual behavior of the male

Sources of information concerning the role of gonadal hormones in the mating behavior of male mammals are identical

with those described above in connection with our discussion of the female.

Puberal changes. In males as well as females of lower mammalian forms puberty is accompanied by a relatively sudden increase in the vigor, frequency and completeness of mating activity. One outstanding difference between the sexes is seen in the fact that male rodents (19, 26, 69), carnivores (36, 75) and ungulates (61) display incomplete mating responses prior to puberty. To be sure this behavior is relatively weak and infrequent, but the fact that it occurs at all sets the immature male apart from his sister, who shows none of the adult female pattern until the first estrus. Of particular significance is the evidence suggesting certain species differences in the amount and completeness of sexual activity exhibited by juvenile males. Immature monkeys and particularly chimpanzees indulge in coital play which approaches the copulatory pattern of the reproductively mature male much more closely than do the fragmentary mating responses of prepuberal rodents (24); and the copulatory acts of immature boys differ qualitatively from that of adult human male only in the absence of ejaculation (73).

The physiological basis for prepuberal sexual responses in males of lower species is not yet clear. Since such activity is not prevented by castration at birth, it cannot be dependent upon the low levels of testicular hormone which exist prior to the attainment of reproductive maturity (22). It is possible that extragonadal androgens, possibly produced by the adrenal cortex, may be responsible, but future investigations will have to settle the point. In any event it is established that immature male rodents are capable of the complete adult copulatory pattern before this response normally appears, for it can be evoked precociously after treatment with gonadotrophins (97) or androgen (19). It is possible that the more extensive sex play of young male chimpanzees and humans reflects a degree of freedom from dependence on hormonal facilitation.

Seasonal changes. Male mammals of seasonally breeding species usually exhibit little or no sexual behavior save during the rut, at which time the testes are greatly increased in size and actively secrete androgenic hormone (75, 113). We are probably safe in inferring that the altered hormonal balance is responsible for the behavorial change, that testicular growth experimentally induced out of season would be accompanied by sexual responses, and that similar results would follow the administration of androgen.

Males of species in which the female is polyestrous are in a more or less constant state of sexual readiness; their testes produce androgen at a relatively steady rate, and we must therefore turn to the effects of castration to gain some knowledge of the ways in which gonadal hormones affect sexual performance in such types.

Behavioral effects of castration. Nearly all of our experimental data on this point are drawn from studies of subprimate species, and here it is apparent that the effects of testicular loss differ according to the animal's age at the time of operation. Prepuberal castration prevents the appearance of complete sexual behavior, although many adult animals gonadectomized in infancy respond to the receptive female with the execution of incomplete mating attempts (15, 95). If mature males castrated before puberty are treated with androgen, they display completely normal copulatory responses (91, 72).[2]

[2] This generalization must be qualified with the provision that normal phallic development has occurred. Male rats castrated at birth and given androgen three months later copulate

Information as to the effects of prepuberal castration upon mating tendencies in male primates would be of great value, but as yet only one case has been described (31). This animal is a chimpanzee which was gonadectomized in infancy. According to the published report prepuberal sexual development was normal, including the usual types of coital play and autoerotic manifestations. Now that the animal is fully adult it reacts to receptive females with a prompt display of sexual arousal and capacity for intercourse. Erection apparently occurs normaly and copulation with intromission takes place without obvious difficulty. The only abnormality is the absence of ejaculation. Administration of androgen to this animal resulted in the appearance of the ejaculatory response and a decrease in the frequency of copulations per time unit (presumably a reflection of the post-ejaculatory refractory period which is seen in males of many species).

The behaviorial changes consequent to castration in adulthood are similar in all subprimate species which have been investigated. Marked individual differences are evident, but in general susceptibility to sexual arousal decreases gradually and the frequency and completeness of the resulting behavior are progressively reduced. Some male rodents (21, 93, 96), lagomorphs (102) and ungulates (96, 106) continue to execute copulatory attempts for six months or longer after castration. This gradual loss of reproductive activity in castrated males stands in sharp contrast to the abrupt and complete elimination of estrual responses in ovariectomized females of the same species. Administration of testicular hormone to males which have been castrated in adulthood restores the normal mating pattern in its entirety (50, 80, 92).

There is unfortunately only one published account of sexual behavior in castrated male monkeys, and this report contains no quantitative data (107). However, it is stated that the copulatory performance of adult monkeys decreases after castration, and potency is said to be lost completely after about six months. There appear to have been no studies of coital activity in male apes castrated after the attainment of reproductive maturity, but the description of the prepuberally castrated male chimpanzee cited above might be taken to suggest that at least some male anthropoids could be expected to continue at a high level of sexual performance despite loss of the sex glands.

Review of the clinical literature dealing with the effects of castration in the adult human male reveals first of all a tremendous range of individual differences. In some cases testicular removal is reflected within a few months in reduced interest in sexual matters and lowered capacity for satisfactory intercourse (35, 77, 79). At the opposite extreme one finds apparently authentic reports of undiminished sex drive and coital ability persisting for several decades (46, 86). In the majority of cases it appears that gonadectomy occasions a gradual lowering of sexual desire coupled with a reduced capacity for sustained erection and particularly for orgasm. Frequently the ability to carry out the sexual act is never completely lost, but the intervals between completed acts become progressively longer (81, 98, 105).

Androgen therapy in the human eunuch usually is effective in restoring normal responsiveness and sexual ability.

This brief survey of the relationships between gonadal hormones and

with great frequency; but very early gonadectomy inhibits penis growth in this species with the result that intromission is rare and the ejaculatory portion of the mating pattern almost never appears (22).

mating behavior in male mammals reveals species differences which parallel those described in the case of the female. The evidence dealing with prepuberal activity and with the effects of either pre- or postpuberal castration suggests that testicular hormones play a more important role in the reproductive performance of lower mammalian species than they do in the primates, and particularly in the anthropoids. In no species can sexual reactions be regarded as independent of androgenic facilitation, but in the chimpanzee and human the behavior which survives in the absence of testicular hormone is much more nearly normal than is that to be seen in castrated males of other species. Some evolutionary shift in the physiological control of such behavior is clearly indicated.

NEUROLOGICAL EVIDENCE

Evidence concerning the function of various parts of the nervous system in mating behavior can be conveniently considered under two general headings: the receptor mechanisms and the effector mechanisms.

The sensory receptors

Because early theories of sexual behavior assigned great importance to genital sensations as primary stimuli, a lot of experimental work has been directed toward a definition of the exact role of such sensitivity in normal mating behavior, and much less attention has been paid to contributions of the distance receptors.

Sensations from the genitals and sex accessories. The once popular belief that the tendency to display sexual behavior is due exclusively to nervous impulses arising in the genitals or other regions of the reproductive tract has been effectively disproven. Copulatory reactions are shown by females of various subprimate species despite congenital absence, surgical removal, or total deafferentation of the entire generative system, provided that ovarian hormones are present (**5, 6, 7, 34**). Similarly males deprived of seminal vesicles, prostate and the associated duct systems display no loss of sex drive (**92**), and deafferentation of the genital region does not abolish mating tendencies (**85**).

Although evidence of this type discredits any attempt to place upon genital sensations full responsibility for sexual responsiveness, it is obvious that under normal conditions sensory impulses arising in the copulatory organs contribute heavily to the intensification of sexual excitement and to the achievement of maximal coital performance. For example, female rats in which the vagina has been removed do not continue to show complete heat behavior, but tend to exhibit a decline of responsiveness in successive contacts with the male (**6**); and male rats in which operative procedures have rendered intromission impossible rarely display the complete mating pattern which includes ejaculation and a post-ejaculatory refractory period (**22**). We must conclude that genital sensations constitute one important source of sexual stimulation although they are not the sole origin for sex drive.

Non-contact stimulation. Relatively little work has been done to measure the contribution of distance receptors to the sexual performance of female mammals (**9, 27**). Nearly all of the experiments dealing with this problem have shown merely that subprimate females are capable of responding appropriately to the male despite experimental induction of blindness, anosmia and deafness. Since the sexually active male plays the dominant and aggressive role in the mating relationship of the species studied, all that such experiments tell us is that a blind, deaf and anosmic

female will execute the postural adjustments necessary to coition in response to the cutaneous, deep pressure and genital stimuli applied by the male. That the entire mating pattern of such drastically desensitized animals can be described as normal is highly questionable, for under ordinary circumstances the sexually receptive female often responds in characteristic fashion to the male long before any physical contact is established. In many species the female orients her display of heat behavior to the male and assumes an aggressive attitude in the courtship pattern if he is slow to respond (28, 44, 110, 116); and it may safely be inferred that responses of this type would be atypically performed or totally lacking in females which were blind, deaf and anosmic.

Studies of sexual arousal and copulatory performance in male mammals have made it apparent that no single type of sensory cue is essential to the occurrence of reproductive responses. Male rabbits and rats continue to display effective coital reactions despite destruction or deafferentation of the receptors for vision, smell, hearing, or touch in the snout and lips and ventral body surfaces (18, 27, 88, 99, 101). There is some reason to believe that loss of any one of these sensory avenues reduces the probability of copulation in the inexperienced male rat, but it is quite clear that none is indispensable (18). When combined operations are performed on male rats, the degree of interference is much more pronounced, and inexperienced animals which are both blind and anosmic rarely mate, although after similar operation the experienced individual usually continues to copulate (17). When three modalities are eliminated (*e.g.*, vision, smell, and cutaneous sensation in the snout, vibrissae and lips) sexual activity disappears (18).

No final conclusion can be drawn from the limited evidence now available but it appears likely that sexual arousal and copulatory performance in the male mammal are products of simultaneous activity in several different sensory systems, and quite probably the natively adequate stimulus consists of a multisensory pattern involving repetitive activation of several receptors.

The effector units

Like all other complex forms of behavior, sexual activity consists essentially of relatively simple responses integrated in a specific sequential pattern; and the exact location of the neural circuits in which the basic sensory-motor integrations are achieved has been studied in some detail.

Spinal mechanisms. It seems very probable that many of the separate elements in the copulatory pattern of females of lower mammalian species are integrated at spinal levels; for female dogs continue to exhibit coital responses despite complete lumbar section (55), and cats in which the cord has been sectioned at the first cervical level display treading, opisthotonus and lateral deviation of the tail in response to stimulation of the perineum (71, 72). The female cat's complete mating posture includes flexion of the forelimbs and it is reported that decerebration just above the pons results in collapse of the extensor rigidity in these members, suggesting the existence of a primitive bulbo-spinal mechanism mediating this element in the copulatory pattern (9).

It is well established that the genital reflexes and certain more complex aspects of the reproductive pattern can be elicited in spinal males. Electrical stimulation of the sacral cord evokes erection and ejaculation in male rabbits and rats (42), cats (90), and dogs (23); and the shock produced by sacral section elicits similar responses in

male guinea pigs (62). In the last named species transection between T12 and L1 is followed within a few minutes by erection and ejaculation accompanied by "rhythmic movements of the ano-genital region" (4). The spinal male cat exhibits priapism in response to tactual stimulation of the ventral body surfaces in the lower abdominal region (43). Male dogs subjected to high lumbar section respond to genital manipulation with the display of erection and ejaculation, and at the same time such preparations exhibit bilateral extension of the knees, ankles and hip joints, depression of the tail and downward curving of the pelvis (87), all of which appear in the copulatory pattern of the intact animal. Genital manipulation of spinal men elicits erection and ejaculation (9) and also evokes a composite response of the abdominal and leg musculature which so closely resembles copulatory thrusts that it has been termed the 'coital reflex' (83).

Diencephalic mechanisms. Nervous circuits located in the hypothalamus appear to contribute heavily to integration of separate responses which comprise the copulatory pattern of female rodents and carnivores, and extensive injury to this brain region eliminates or or interferes greatly with the female's normal adjustments to the sexually aggressive male in the case of the cat (10), the guinea pig and the rat (39, 48).

The only published study which deals with the effects of injury to the hypothalamus upon mating behavior in male mammals indicates that damage to the medial half of this region tends to 'depress' sexual behavior in male rats, although the area apparently contains no structure essential for the integration of the mating pattern (30).

Forebrain mechanisms. Injury to or complete removal of the cerebral cortex, hippocampus, and caudate-putamen complex does not abolish coital activity in female guinea pigs (39), rabbits (27), rats (37), or cats (8). In fact these are indications that destruction of the neocortex may lower the threshold and increase the frequency of separate estrous reactions, for decorticate female rats show a heightened tendency to assume the copulatory position, display ear vibration more readily and exhibit a decrease in the frequency in the back-kicking response with which the intact female occasionally repulses the male (20). It has been reported that the behavior of female rhesus monkeys subjected to bilateral temporal lobectomy is characterized by an increase in willingness to receive the male and a raised frequency of masturbation (64).

Although the separate sexual responses survive in decorticate females, the operation is not without effect upon the total mating pattern, for female rats lacking the neocortex fail to orient their receptive responses toward the male, and the timing and integration of the individual reactions usually are disrupted (20).

It has been reported that fertile mating can be obtained in decorticate male rabbits (27) and rats (37), but in neither of these two studies were quantitative measures of sexual behavior employed, and the completeness of neopallial removal was not checked by examination of the sectioned brains. When both of these desiderata were met in investigations of the sexual activity shown by male rats after cortical injury, it was found that extensive invasion of the neopallium unquestionably exerts deleterious effects upon reproductive behavior (12). The locus of the lesion is unimportant and the critical factor is the amount of tissue removed. Injury involving less than 20 per cent of the neocortex does not eliminate copulatory responses, but when the loss increases to 50 per cent sexual activity is abolished in some indi-

viduals and survives in others (21). In fact as the amount of cortical destruction increases above approximately 30 per cent, there occurs a progressive decrease in the proportion of males continuing to mate; and when the extent of bilateral invasion exceeds approximately 75 per cent of the total neopallial mass coital reactions are totally eliminated (13). Even though some male rats deprived of half of the neocortex continue to mate, they do so in a relatively small proportion of their postoperative tests, and the percentage of positive tests appears to be inversely proportional to the extent of cortical destruction.

The exact nature of the cortical contribution to a sexual behavior in the male rat is not clear but it is obvious that the cortex is not essential to control of the motor pattern, for when brain-operated individuals copulate they do so in perfectly normal manner (12). Studies of the effects of restricted cortical injury upon sensory capacities in rodents, and investigations of sexual activity in peripherally desensitized males suggest that the absence of sexual behavior in decorticated animals cannot be explained purely as a result of interference with major sensory pathways or areas of representation (21).

Inasmuch as cortical injury appears to decrease sexual responsiveness without seriously affecting either the capacity for reception of stimuli or ability to execute the motor acts of courtship and copulation, it has been suggested that the cortex serves to maintain the excitability of noncortical neural mechanisms responsible for the organization of the male's mating pattern. This interpretation receives indirect support from observations to the effect that some males which cease copulating after partial decortication exhibit a return of sexual activity in response to injections of androgen (12). These findings indicate that unidentified subcortical mechanisms become more excitable under the influence of the exogenous hormone, and that the artificially raised hormone level compensates for loss of facilitative impulses normally provided by cortical activity.

The fact that extensive neocortical injury eliminates sexual activity in male rats but fails to abolish fertile copulation in females of the same species is worthy of comment. The most obvious interpretation of this inter-sexual difference rests upon the fact that the female's is primarily a passive role, in which the assumption and maintenance of certain gross postural adjustments are the only indispensable elements. However, there seems to be more to the story than this, for it must be recalled that decorticate female rats give evidence of an *increased* frequency of heat responses and a lowering of the threshhold involved in their elicitation.

One study of the effects of partial decortication on mating behavior in male cats has shown that animals suffering bilateral removal of the frontal and prefrontal areas exhibit no reduction in sexual excitability but do experience difficulty in achieving the proper orientation to the receptive female (67). Although such animals occasionally may achieve complete copulation, in the majority of instances the sensory-motor impairment consequent to brain injury is reflected in poorly integrated and biologically ineffective attempts to grip and mount.

Essentially similar results were obtained in a more extensive investigation which Dr. Arthur Zitrin and I conducted but have not yet published. We found that the mating behavior of male cats survived bilateral removal of the frontal, temporal, parietal or occipital lobes. However, although they occasionally copulated normally, animals with such lesions often exhibited disoriented and uncoordinated sexual re-

sponses. Cats deprived of one cortex and the frontal pole of the opposite hemisphere made repeated attempts to copulate but were unable to effect union unless they were placed upon the receptive female, in which case the pattern was completed normally. Bilateral occipital lobectomy eliminated reactions to the distant female, but males sustaining such lesions displayed normal coition as soon as they came into any sort of physical contact with the estrous queen. We found that after total decortication male cats failed to make any response to the female even when they were placed upon her, and other workers have reported total loss of sexual behavior in decerebrate male cats and dogs (10).

In carnivores as in rodents it appears that the importance of the cerebral cortex to mating behavior is subject to a marked intersexual difference, for as described above female cats and dogs are capable of fertile mating after loss of the entire telencephalon.

Comparison of the effects of neocortical injury upon sexual performance in male rodents and carnivores reveals certain differences which reflect the higher degree of encephalization obtaining in the latter order. Sensory and motor capacities depend more heavily upon the cortex in cats than in rats, and it is therefore not surprising that removal of primary sensory areas has more serious effects in the former species. Similarly, the finer motor adjustments involved in copulation suffer greater interference after precentral injury in cats than after loss of the entire frontal pole in rats.

Are we then to conclude that the depression of mating tendencies seen in decorticated or decerebrated male carnivores is due exclusively to interference with the primary projection areas for sensory and motor functions? Such an interpretation is probably an oversimplification. Animals sustaining very large cortical lesions fail to make any response whatsoever to the estrous female although they are capable of reacting effectively to various environmental stimuli such as those involved in finding and eating their food, and this seems to argue for a lowering of sexual excitability *per se*.[3] Supporting evidence is not yet available, but it may be suggested tentatively that in the cat as in the rat impulses from the cortex exert facilitative effects upon subcortical sexual mechanisms rendering them responsive to external stimulation.

There have been no systematic investigations of the effects of cortical injury upon sexual activity in any primate species, but existing knowledge concerning the effects of various types of lesions upon other behavioral patterns permits the assumption that extensive cerebral destruction would seriously interfere with or abolish coital responses in male monkeys and apes. If for no other reason this seems probable because the pronounced sensorymotor loss following destruction of the primary and secondary projection areas almost certainly would preclude accurate orientation to the female or execution of the behavioral adjustments necessary to sexual intercourse.

Presently available evidence is extremely fragmentary but it may be predicted that future investigations will support the generalization that the forebrain, and particularly the cerebral cortex, have come to play an increasingly important role in the control of courtship and mating responses of mammals. The most obvious type of change at ascending levels within the mammalian class lies in the growing influence of cortical areas of representation for sensory and motor activities; but increasing cortical control of any type

[3] It is of course obvious that responsiveness to many nonsexual stimuli is also affected.

of response often brings about secondary changes in the nature of the adequate stimulus and in the pattern of overt response. Evidence indicating that such changes have occurred in the case of sexual behavior will be considered briefly at this point.

BEHAVIORAL EVIDENCE

The results of certain nonphysiological studies of sexual behavior appear to bear directly upon the interpretation of the physiological experiments cited above. These are concerned primarily with the effects of external stimulation upon sexual manifestations in males and females of various mammalian species from rodents to anthropoids. The first body of evidence has been mentioned earlier in this discussion. It deals with the frequency and completeness of sexual responses shown by prepuberal individuals, and it will be recalled that infantile sex play occurs with greater frequency and takes a more nearly adult form in the primates than in any lower species. It appears likely that this behavioral difference reflects an increased importance of cortical function and a concomitant reduction of hormonal control over sexual behavior in the primates.

Inter-sexual differences in lower mammals

Although neither males nor females of subprimate species exhibit complete mating behavior prior to puberty, the juvenile male does show some sexual responsiveness whereas the female's prepuberal behavior includes none of the sexually receptive pattern. The possibility that this variation is related to differential importance of the cortex to the two types of response is clearly indicated.

In male rodents and carnivores sexual arousal tends to be inhibited in a strange environment although comparable interference occurs much less frequently if at all in the female. Male rats placed in a strange cage with a fully receptive female do not ordinarily proceed to mate at once but spend a great deal of time exploring the environment and may not copulate until they have been in the cage for a considerable period. Estrous females, in contrast, respond to the male almost at once, and mate as readily in new surroundings as in their own living cages. Similar inter-sexual differences are seen in various carnivores such as the mink (2, 65) and coyote (40). The receptive female cat mates readily during her first test under laboratory conditions, but males of this species rarely copulate when they are first put in the testing room and offered a female in heat. Often it is necessary to manipulate the experimental situation in order to induce the initial mating; although once this has occurred, the male displays spontaneous courtship and copulation in subsequent test periods (119).

The converse of environmental inhibition of sexual responsiveness is seen in the behavior of male rats and rabbits which attempt to mate with almost any stimulus animal which is presented in an environmental setting previously associated with normal copulation. Males of either species which have copulated frequently with receptive females in a particular cage tend to attempt coition with males, non-receptive females or even with animals of a different species when such stimulus objects are encountered in the original testing situation (11, 27, 63, 99).

The sexual responsiveness of the male may be depressed in an environmental setting previously associated with conflict or pain. Neurotic male dogs are slow to mate with the estrous bitch presented in the experimental room where the neurosis was induced, although in the paddock copulation may occur

promptly (52); and male rats subjected to electric shock during or immediately after copulation usually fail to mate in subsequent tests (111). Male marten (75), mink (65), and foxes (44) which are being trained for stud and are attacked by the female in the course of early services often refuse to mate when they are subsequently offered more tractable partners; but in the case of experienced sires the high level of arousal induced by previous conditioning apparently overrides any such inhibitory effects, and coition usually is accomplished despite temporary resistance on the part of the female. In the case of the female previous experience seems to have little or no effect upon willingness to mate in succeeding estrous periods.

The facts that extraneous stimuli tend to interfere with the male's reactivity to the receptive female but have little effect upon the behavior of the female herself, and that previous experience may lower or raise the male's susceptibility to sexual arousal although it does not alter the responsiveness of the female may well be related to the finding that the cerebral cortex is intimately involved in the copulatory behavior in the male but is less important to the coital adjustments of the female. In the case of the male a profusion of nonsexual stimuli may evoke within the cortex a series of activities incompatible with those essential to sexual responsiveness, with the result that the subcortical mechanisms mediating courtship and copulation receive no facilitative impulses from higher centers and therefore fail to react to external stimulation. Conversely, stimuli which originally possess little or no relation to sexual excitability may, by a process of cortical conditioning, become associated with sexual mechanisms and thereby assume sexually-exciting qualities. Since the subcortical nervous circuits in which the female's responses are integrated are less closely related to the neocortex, activities in the latter brain region rarely influence the excitability of the lower centers.

In the absence of experimental evidence to indicate the effects of cerebral injury upon sexual performance in primates of either sex we cannot know whether the inter-sexual differences obtaining in subprimate species have their counterparts in the higher forms. However, as has been pointed out previously, it appears highly probable that the marked tendency toward encephalization which characterizes the primate nervous system renders certain cortical areas essential to the execution of coital reactions in both sexes. It may be assumed with reasonable assurance that, in the anthropoids at least, the cerebral cortex makes important contributions to sexual excitability and mating behavior in females as well as males.

One very suggestive bit of evidence concerning the possible effects of cortical influences upon sexual performance in male apes lies in the observation that some chimpanzees have to learn to copulate. It has been noted that sexually mature but inexperienced males placed with the receptive female show signs of marked sexual excitement, but the resulting attempts to accomplish copulation usually are unsuccessful. The naive male appears incapable of carrying out his part of the mating act and it has been suggested that a great deal of practice and learning are essential to biologically effective coition in this species (116).[4] Adult male rodents which have been reared in isolation copulate normally the first time they

[4] Female chimpanzees lacking previous sexual experience respond effectively to experienced males and mating is carried out normally. Here is some slight indication that even at the anthropoid level the neocortex may be less important to the sexual activity of the female than to that of the male.

are offered an estrous female. It is possible that increasing control of sexual behavior by cortical mechanisms has resulted in a reduction of the degree to which coital activities can be executed in the absence of specific sexual experience. In other words, as the cortex assumes more and more of the responsibility for organizing sexual responses, such responses may become progressively more dependent upon previous experience of the individual.

CONCLUDING REMARKS

We have cited evidence which shows that susceptibility to sexual arousal and capacity for coital performance in lower mammals depends heavily upon hormones from the reproductive glands, and that in higher species, particularly apes and humans, the rigidity of such hormonal control is relaxed sufficiently to permit a considerable amount of sexual responsiveness and potency in the complete absence of sexual secretions.

We have also reviewed a few studies which seem to indicate (although certainly not to prove) that by virtue of phylogenetic increase in the cortical direction of all complex sensory-motor integrations, the sexual behavior of higher forms has become much more dependent upon activity within the cortex than is that of lower species.

Finally, we have seen that at subprimate levels cortical function is more important in the sexual behavior of the male than in that of the female; and it has been pointed out that in rodents and carnivores the male's mating tendencies are subject to inhibition or facilitation by a wide variety of environmental conditions, whereas the female's sexual responsiveness is relatively independent of nonsexual exteroceptive factors.

Fragmentary as it obviously is, this evidence can be used to formulate a rather interesting and perhaps useful thesis. It may be suggested that in the course of mammalian evolution as the cerebral cortex assumed a more and more dominant role in the control of all complex behavior patterns, it came to exert an increasing influence over more primitive neural mechanisms which originally possessed sole responsibility for the mediation of sexual activities. As the latter mechanisms became progressively more dependent upon facilitative impulses from the neocortex, gonadal hormones, which once served the indispensable function of maintaining excitability in the lower circuits, tended to decrease in importance. Finally, by virtue of their growing reliance upon cortical facilitation, the subcortical sexual mechanisms became susceptible to excitation or inhibition through a wider and wider variety of stimulating conditions, with the result that in the human they may be activated by stimuli possessing no biologic sexual significance and their excitability may be so depressed by extraneous factors that they sometimes fail to respond in biologically adequate situations.

These ideas can be rephrased in terms of the general problem with which this symposium is concerned. Heredity, as represented by the relatively stereotyped and inflexible functions or capacities of the subcortical neural mechanisms and the gonadal hormones, plays the major role in the courtship and mating of subprimate species. Environment or experience, as it affects the more modifiable cortical functions and the capacity of cortical activity to alter the responsiveness of lower centers, is of primary importance in the sexual behavior of the higher mammals.

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THE GROWTH OF THE SENSORY CONTROL OF BEHAVIOR BEFORE BIRTH

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One of the world's most eminent biologists, G. H. Parker, wrote last year: "I have often tried to evaluate that which we have by birth and that which we acquire from social contact, and I have concluded that we are perhaps about nine-tenths inborn and one-tenth acquired." This same writer further says: "In a measure this deflates the educator's balloon, but we must remember that what education gives us counts tremendously in everyday life, so much so that we certainly overestimate it in the balance of human totalities. What we get by education is a small acquisition planted on a very large inborn background" (14).

It is hard to cite any facts, biological or psychological, which refute this statement by Professor Parker. Nevertheless in technical writing in the fields of social psychology, sociology, and cultural anthropology in recent years this hereditarian point of view has not been fashionable. It is important, therefore, in this symposium to re-evaluate some of the evidence concerning at least that aspect of the development of behavior which is almost certainly independent of learning and the influence of society.

A knowledge of that which is inherited and that which is culturally acquired in human behavior is of practical importance today. Information of this sort, when it is factual and not mere opinion, is basic to a realistic program directed toward the ultimate goal of the formation of a society in which men everywhere may live peacefully in a world of interdependent cultures.

The present paper is devoted to a brief survey of some of the recent evidence which has been collected concerning the onset and growth of the very early behavior of the individual. To put this in another way, this paper is concerned with those early beginnings of behavior and mental life in the individual which, in Professor Parker's sense, are prior to the first effective influences of education or of society.

Sir Charles Bell, Johannes Müller, and Ludwig von Helmholtz (2, 13, 8) long ago pointed out that our senses give us the effects of the external world and not in a direct way a knowledge of things in themselves. Thus in studying the natural history of mind as it develops in each human individual, an understanding of the growth of the effectiveness of the senses is clearly fundamental to one who would understand early psychological processes.

The investigator who attempts to study the senses before birth finds many of the standard experimental methods of psychology unavailable. The unborn child cannot tell the experimenter what his experiences are by the use of words. Thus at once some of the main traditional methods for the study of sensory capacity are excluded. There is also no reliable evidence that the conditioned-reflex techniques which have been a mainstay of objective psychology can be used in the study of the senses in prenatal life. There are some suggestions, it is true, that conditioning of a sort can be established in the unborn human fetus. No one has yet shown, however, that this technique can be used as a method of studying the senses in a quantitative way before birth. The whole special series of con-

ditioned-reflex techniques which from the early days of Pavlov's laboratory have been used in many countries with much success in the determination of sensory thresholds and in the study of other sensory capacities in infrahuman animals and man are, therefore, closed to the investigator of the senses in fetal life. All other experiments which depend on learning are also inapplicable at this early period.

The student of the onset and early development of the sensory capacities of the fetus is thus driven back to a utilization of those reactions of the organism which can be observed or recorded, which are released by the stimulation of the sense organs or receptors, and which are inborn and initially, at any rate, free from any modification by learning or the effect of experience. In the title chosen for this paper, 'The Growth of the Sensory Control of Behavior before Birth,' one sees essentially a description of the one basic technique that may be used in the study of the senses in very early life. It is not too much to say that this is the principal method of investigation of any aspect of what one may wish to call mental life of the prenatal and probably also of the early neonatal mammalian or human organism.

There are a number of basic conditions which should be observed in such studies. The organism under investigation should be maintained in as nearly normal a condition as feasible, and the nature of the stimulus and the related response should be as accurately measured as possible.

The late Sir Joseph Barcroft in an experimental investigation of the fetal life of typical large mammals (1) has clearly pointed out the importance of maintaining the fetal organism in a condition such that the so-called internal environment of its own blood stream is constant and normal. This is a requirement which may well be applied at any stage in the development of an organism when its responses are to be studied and compared. The oxygen saturation of the blood, to take but a single example, has been shown to be of the greatest importance in determining the threshold of activity in the central nervous system and consequently in determining the pattern of stimulus-released muscular responses of the organism in question.

The consideration of the importance of the internal environment, therefore, at once raises a question which is of significance to one who would study behavior in prenatal life. This question is whether or not all behavior in the fetus is determined by processes which are released by stimulation of receptors by energies external to the organism or whether some behavior that is observed is the result of internal changes initiated by the internal environment of the central nervous system of the growing organism. An experimental attack upon this question is not easy. There are many technical difficulties in maintaining constant conditions such as a fully normal blood supply in mammalian fetuses that have been exposed for study. Some of the most interesting approaches to this problem have therefore been made by observing the growth of behavior in inframammalian types. The embryos of fish and salamanders have been especially useful in such studies. These organisms feed themselves during early growth by utilizing the yolk of the egg from which they have initially developed. They can be studied in water during the whole period of embryonic growth. They can be continuously observed from the single cell stage to the period when they are motile and self-maintaining organisms, without operative interference.

Observations can be made of the onset and development of behavior in such

organisms in a most objective manner. Experiments on such organisms can be easily repeated on large numbers of genetically very similar individuals. For example, some years ago I raised parallel groups of drugged and undrugged salamanders. These small organisms, incidentally, were, I believe, the first animals ever used for experimental purposes in the then just-opened Eno Hall Laboratory of Psychology of Princeton University. These experiments (3, 4, 5) demonstrated that the growth, or maturation of behavior, goes on in approximately the same manner in developing salamanders whether they are allowed to respond actively to their external environment or whether by continuous anesthesia they are allowed to grow but not to respond at all until control groups have long been free-swimming. In the organisms studied in these experiments there is no substantiation to the theory that the stimulus to effective growth of the response mechanism is use.

The late G. E. Coghill, one of the great students of the correlation of anatomy and behavior, studied salamander embryos in great detail. He showed that the muscles of these tiny vertebrates first develop to a point where they can be independently stimulated before any neural mechanisms are ready to activate them (7). It is probably not too much of a generalization to say that this sequence is typical of most developing organisms.

The question has been raised as to whether or not in any organism at any time centrally aroused behavior resulting from changes in the internal environment develops before the total receptor-neuromuscular mechanism is complete. Let us look at this problem. There seems to be evidence that in certain fish embryos and probably in many other types of fetal organisms such centrally aroused responses do indeed take place. Certainly in theory there is no reason why a chemical change in the blood should not so alter the internal environment of a growing organism as centrally to initiate activities in its motor nerves. Such reactions might well take place before the full receptor-neuromuscular mechanism has reached functional maturity.

Even when the total mechanism has developed there is also no reason why centrally initiated behavior unrelated to external sensory stimulation should not take place. The present knowledge of the effect of carbon dioxide and of oxygen lack upon the respiratory centers of the brain and upon receptors in the carotid sinus may give some idea of the possible complexity of the causal chain in the central initiation of behavior. Barcroft and most other writers who have dealt with this question point out the difficulty of deciding in a given case whether an external response is in all respects centrally *aroused* or merely dependent upon an altered threshold of excitability in the central nervous system which changes the effect of what might well be a constant inflow of sensory nerve impulses dependent upon continuous external stimulation.

H. C. Tracy (16) has studied the early development of behavior in typical fish embryos. He seems to have demonstrated that, when external conditions are maintained in a relatively constant manner, the behavior shown by these growing fish is largely internally determined by the changing blood chemistry resulting from the organism's own metabolic processes. From this point of view it seems that the activities of these young fish in their external environments are in some ways similar to the rhythmic beat of the developing heart cells of all vertebrates. It is now well recognized that before specialized neural structures have developed, the primitive rhythmic activity

of what will later be the mammalian heart begins. In man, for example, such activity starts at about the third week after insemination. This rhythmic heart activity is complexly determined, but it may be described as a result of the building up and sudden release of processes which are related to the metabolism of the embryonic heart cells as they maintain themselves in their chemical and cellular environments. This process has been compared to that of an automatic syphon. In the model of such a system a continuous small stream of water flows into a tank. The water level of the vessel gradually rises. At a given point the whole container is quickly emptied by the syphon. The level then gradually begins again to rise until it once more reaches the discharge point, and so on. In this manner a continuous process becomes periodic.

The beat of the primitive heart cells of the embryo and even the activity of the total fish embryo when living in a relatively constant environment may be related to a comparable continuous series of processes which lead to rhythmic discharges. Thus it may be that the total integrated organism may 'beat,' as it were, in a more or less rhythmic manner while maintaining itself in a constant external environment. Such behavior in only a most indirect way can be considered to be specifically 'receptor-released.'

This conception is important in thinking about the nature of all truly external receptor-controlled behavior in early life. To put this in its simplest terms, it is important to remember that the growing organism is never in any way passive when it is stimulated. The famous inanimate statue of Condillac, which was supposed to take on mental processes one by one as it received its different senses, is a philosopher's dream and not a biological or psychological reality.

There is reason to believe that the continuous intrinsic rhythms of the central nervous system in fetal and indeed in adult organisms as recorded in electroencephalograms are not unrelated to the sensory control of behavior. In collaboration with other investigators I have been able to show that the clamping off of the placental blood supply to a guinea pig fetus almost at once abolishes certain cortical electrical rhythms (6). These rhythms had previously been easily recorded. When these rhythms stopped—and inferentially the cortical activity of which they were a sign also stopped—another change in behavior took place. The muscular responses of the limbs which could be initiated by stimulating the skin of the paws, for example, became more violent than they had been when cerebral activity was at its best. To put this in another way, when the internal environment changed so as to remove the inhibiting functions of the higher nerve centers, the behavior dependent on lower centers changed.

The present writer and his associates (6) have developed a constant temperature bath and other experimental procedures so that fetal cats, guinea pigs, and other mammals can be studied, often for long periods, under conditions which are at least in some respects normal. In such an experimental setting it is possible to stimulate the mammalian fetus with stimuli of known physical characteristics and to record the resulting responses on the film of a properly placed motion picture camera held firmly above the experimental table. Recording of this sort makes possible at least an approach to quantification, as repeated study and measurement of the motion picture record are possible when the experiment itself is over.

This convenient experimental arrangement can be used with infrahuman mammals, but it is not in the same way

appropriate for the study of human fetal material. The work of M. Minkowski (12) and the brilliant recent work of D. Hooker (10), Barcroft, and other investigators upon living human fetuses are, however, of great importance. Human fetal material is available only for study when pregnancy must be interrupted to preserve the health of the mother. This means that almost always placental circulation has been interrupted before the fetus can be studied. Sometimes also the anesthetic given to the mother spreads through the blood stream and drugs the fetus. In spite of these shortcomings, the schedule of the onset of specific sensory and motor processes in the human fetus is of course peculiarly significant for all whose primary study is the growth of behavior in man. On the other hand, the general processes of development and of the onset of sensory control of behavior can be studied more advantageously in infrahuman mammals. In such organisms the internal environment can be held much more constant than it can be in the typically available human fetal material, which is almost always undergoing progressive asphyxiation during all experimental periods.

The study of the growth of the effectiveness of receptor mechanisms in guinea pig fetuses which the present writer and his associates have carried out may be taken as an example of the study of the behavior of the mammalian fetus. These studies have allowed repeated experiments upon large numbers of organisms at each developmental stage. This work has made it possible to say that known external stimuli of a number of types tend to release patterns of behavior which are remarkably specific to each receptor field or zone that is being stimulated. A simple statistical approach has thus been made possible to the problem of the stimulus control of behavior, as repeated experiments under relatively constant conditions have been possible on fairly large numbers of organisms.

This study (4) has convinced the present writer that specific receptors of the organism will, when comparably stimulated, often release amazingly specific responses. To put this in another way, when a given reflexogenous zone of the skin of a fetal guinea pig is stimulated, a definite response tends to take place. This seems to be true at all developmental levels after the receptor mechanism first becomes functional. Such responses are of course often masked by the effect of concomitant external stimulation or by other centrally initiated processes which are going on at the same time that the experimental stimulus is applied. But by repetition of the experimental stimulus in many organisms, patterns of behavior that are constant can be isolated and described which are apparently typical of the receptors that are stimulated.

The importance of the intensity of the stimulus must not be lost sight of in such work. The present writer has been able to show, for example, that there is a quantitative relationship between the intensity of the tactual pressure stimuli and the extent, generality, and pattern of elicited response. This is also true at all fetal developmental stages that have been studied. Similar experimental results have been secured from temperature stimuli. Drops of liquid that varied in temperature above and below the physiological zero of the organism were applied to specific skin zones and a constant relationship between intensity of the stimulus and the resulting response was established. Stimuli which are just intensive enough to call out a response bring out most consistently the response which is, as it were, most typical of the point stimulated.

It should be noted, however, that at certain periods of development, for example, a supraliminal stimulus on the pad of the forepaw may lead to what the distinguished Princeton psychologist E. B. Holt called an *adient* response (9). This means that the paw is thrust forward as if to get more of the stimulus. At the same time and in the same organism a more intense stimulus may elicit an *abient* response, which tends to remove the member from the region of the stimulus.

The scope of this paper will not allow a review of the work that my associates and I have done on sensory fields other than the skin. Nor can the work of many other investigators such as W. F. Windle (19) and Z. Y. Kuo (11) be reviewed. Responses elicited in fetuses to the stimulation of the nonauditory labyrinth and the responses to auditory and visual stimuli are of course interesting and important. In such work at times direct recording of the bioelectric phenomena associated with the activity of the receptor and of the related response to stimulation has made possible the understanding of new functional relationships. The study in the fetus of the onset of the Wever-Bray effect—named for two distinguished psychologists of Princeton—is typical of such work. In this connection A. F. Rawdon-Smith, Bertram Wellman, and I (15) were able to show that the electrical response of the cochlea can first be recorded in the fetal guinea pig at just the same stage that airborne sounds first stimulate the auditory mechanism of the fetus so as to initiate externally observable startle responses.

In general terms, the course of the prenatal development of fetal motility in a typical organism such as the guinea pig fetus can be summarized briefly. Such responses develop from a first twitch of the neck and shoulder at about 28 days after insemination to an active and effective and apparently purposeful and extremely varied repertory of adaptive behavior acts by about the 53rd postinsemination day, or about a week before normal birth.

The late guinea pig fetus shows behavior which indicates its adaptability to changing external environmental situations. In fact, a few days before birth the normal fetal guinea pig has many characteristics which have led comparative psychologists to attribute mental processes to infrahuman organisms. Similar reactions are noted in the human fetus, and here surely such responses must be thought of as the onset of the mind of the growing individual. If, therefore, we are to speak of the beginning of mind or of mental processes or of intelligent behavior in connection with early adaptive acts, it can be said that during the period of late fetal development in the guinea pig such reactions are certainly already present.

Let us glance back at this amazing development again. When the fetus first begins to respond to external stimuli, it is a living, integrated system including effective receptors, peripheral and central nervous system, and muscles. Just before this the muscles alone can in some and possibly all types be stimulated directly. Then as a result of neural growth, probably in the central nervous system, sensory stimulation comes to release behavior. This release, however, is conditioned by three sets of factors: (1) the nature of the stimulus, (2) the anatomical make-up of the living systems involved, and (3) the chemical state of the internal environment of the organism at the time. In such reactions, however, there are discernible inborn and very specific patterns. An example may make this clear. In late prenatal life when a quantified pressure stimulus such as a

hair esthesiometer is applied just below the ear of a fetal guinea pig, a local pinna or ear reflex twitch typically occurs. If the stimulus is repeated or is allowed to persist continuously, the paw on the same side that is being stimulated is almost always raised in such a manner as definitely to localize the stimulus. Often the paw effectively brushes the stimulus away. If the experimenter persists in holding the experimental hair on the place stimulated after the paw has brushed by, the whole head and trunk of the fetus may be rotated. At length, if stimulation still continues, almost every muscle of the organism may be called into action. Swimming is then initiated to move the animal as far as possible in the experimental bath until such self-activated movement is inhibited by the increased tension of the umbilical cord.

Almost any observer who watches this sequence will call the behavior he observes purposeful and end-seeking. It is the fetal basis of the proverb "If at first you don't succeed, try, try again." Such behavior seems to be teleological if any behavior is. But there is no evidence that any of this behavior is learned. There is no reason at all to think of it as the result of the individual experience of the fetus in question. If time allowed, it could be shown from experimental evidence why it is almost certain that such responses are prior to and independent of any opportunity for practice. It may be said that the dynamic processes of embryological growth have produced an organism the structures of which must respond in this way when stimulation of the sort just described occurs for the very first time. The beautiful, marvelously variable, adaptive, and supple responses of the late fetal guinea pig, or the human fetus for that matter, can thus be seen as dependent upon the serial activation of inborn structures.

Birth makes many changes in the growing organism's patterns of behavior. Direct breathing produces a better oxygen supply for the blood, and the many new stimuli of the external world effect many changes in behavior. But birth does not suddenly alter the basic patterns of the nervous system. These patterns were growing before birth and continue to grow after birth. This growth is largely the result of processes which are in the last analysis dependent on heredity and not upon individual experience.

Visual stimuli after birth for the first time effectively act upon the retina of the eye, but experiment has shown that the visual mechanism can be activated in certain ways, at any rate, in late fetal life if effective light stimuli are present. This fact illustrates what is probably a basic law of behavioral development. In the growth of behavior most systems can function, at least to some extent, before they are adaptively needed by the organism to advance its life processes. This preparation of mechanisms before they are called upon to function almost certainly continues after birth. Many of the new responses shown by the growing child and by the adolescent are quite probably the result of such maturational processes and not alone of learning, although soon after birth learning comes to be interwoven in a most intimate way with much behavior growth.

About a quarter of a century ago the pendulum of theory in psychology made a violent and at the time a most necessary swing away from a belief that inheritance was a mysterious force alone determining many adult mental characteristics. But it now seems almost certain that, as is so often the case, this pendulum of theory has swung too far. As recently as 1930 J. B. Watson, one of the leaders in the anti-instinct movement, was still writing: ". . . there is

no such thing as inheritance of capacity, talent, temperament, mental constitution and characteristics" (18). Investigations of the sort outlined above in this paper show how mistaken this assertion now seems to be.

Today it is becoming more and more clear that during the whole period of growth and even during maturity, and again especially in the decline of capacity in old age, the behavior of an organism can always be seen as resulting from the changes of structure and function which in the last analysis are in part at any rate the result of inherited patterns. Some of these responses seem only secondarily to be dependent upon learning and individual experience. Facts of the sort presented in this paper make another of Watson's statements, made in 1928, "there is nothing from within to develop" (17), sound strange indeed. Many other statements of a similar sort and of more recent date could be quoted from writers in social science fields.

Contrary as it is to the extreme views of the anti-instinct writers of the 1920's and the current dogma of some social scientists, there is nothing that I know of in the recent quantitative study of the early growth of behavior which tends to deny the possibility of the truth of the statement quoted at the beginning of this paper that human nature is nine-tenths inborn.

This paper as its contribution to the symposium may, therefore, conclude that continued study of behavior which is clearly the result of maturation is definitely worth-while. Study of this sort must at some time include more objective and scientific investigations of inborn individual and racial *differences* of behavior than have ever been made. This means, it seems, that sociology, cultural anthropology, and social psychology may well devote as much study as possible in the years that lie immediately ahead to the investigation of those fundamental aspects of human behavior which cannot be understood without a knowledge of heredity and the science of genetics and of what may be called the embryology of behavior. Studies of this sort can be carried on without denying at all that learning and cultural conditioning are important in a *full* explanation of almost every adult human psychological trait. The point of view that is being suggested merely proposes that cultural and environmental determinants not be asked to try to carry the whole task of explaining all of human nature. To put this in another way, biological, psychological, and social science must ever be on guard against a disproportionate emphasis upon either nature or nurture.

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STRUCTURAL VARIATION IN THE NERVOUS SYSTEM IN RELATION TO BEHAVIOR

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A few days ago, outside my laboratory window, were the webs of two crab bellied spiders of the genus *Gasteracantha*. Both webs were perfect orbs, one almost two feet in diameter with foundation lines nearly twelve feet in span, the other scarcely two inches across, spun in the fork of a twig. Both webs were decorated with white flocculent tufts, spaced at exact intervals along three lower radii and along the foundation lines. Except for the difference in size the webs were duplicates almost to the minutest details. Their builders, clinging to the characteristic open hubs of the orbs, differed in size almost as much as did the webs, and their odd crab-shaped bodies were also duplicates in form and coloration. The ornamented web, perhaps the most beautiful of those spun by the orb-weavers, is as characteristic of the genus as is the body form, and the activities by which it is constructed are as certainly determined by heredity as is the body structure.

The student of animal behavior, who sees on every hand the genetic determination of such elaborate physical and behavioral patterns, is naturally prejudiced toward stressing hereditary factors in behavior. Discussions of heredity and environment have tended to ignore species-constant characters and to consider only individual differences, yet the behavior traits which are present in all members of a species give, in many ways, the most illuminating data for the problem of heredity, since they illustrate the varieties of behavior which can be so completely determined by genetic factors as to be independent of the normal range of environmental influences. Species-constant characters include not only reflexes and such complex instincts as are exhibited by arthropods and birds, but also differences in the level of activity, in motivation, in sexual and maternal patterns of behavior, in emotional and temperamental traits, and in general and special abilities. There is scarcely a variable in the range of human personality which cannot be matched as a fixed interspecies difference in other animals.

Interspecies differences in behavior must be referred to differences in structure and these, with few exceptions, are to be sought in the nervous system. Even where the behavior is dependent upon the structure of effectors, such as the various types of spinnerets possessed by different genera of spiders, correlated differences in nervous structures are essential to their efficient action. Conversely, structurally similar organs may differ enormously in their utilization. The chimpanzee hand is capable of all the elementary movements of the human hand, yet is used scarcely more effectively than the rat's paw.

A comparison of the kinds of differences in brain structures existing among different species of animals with the variations in structure which occur within a single species should provide some clue to the genetic determination of individual differences. Interspecies differences are obviously a result of hereditary constitution, and, if the same kinds of structural differences are found to oc-

cur among individuals of a single species, they justify the inference of genetic determination of corresponding individual differences. A proposal to make such a comparison is, unfortunately, a statement of a research program rather than a project which can be carried out on the basis of known facts. Knowledge of the exact function of various nervous structures is extremely limited and few studies of individual variations in the nervous system have been made. An attempt to relate phylogenetic and individual differences in behavior to brain structure is therefore rather an adventure in correlating the mysterious with the unknown. Nevertheless, a summary of evidence on these matters has present value in pointing out essential problems of neuropsychology and in stressing relevant facts which are generally disregarded in evaluating evidence on the problem of nature versus nurture. I shall review some major similarities and differences in brain structure as they appear between species and between individuals, to show that individual variations are essentially similar to interspecies differences and may, by analogy, be assumed to determine corresponding individual characteristics of behavior.

STRUCTURAL CONSTANCY OF THE NERVOUS SYSTEM

The general plan of brain structure is remarkably constant throughout the mammalian series. The distribution of sensory tracts, the number of receptive nuclei, and the arrangement of functional areas of the cortex vary little from the marsupials to man. The precision in arrangement of anatomic structures in the brain has only recently been appreciated. The physiologists of the last century postulated the projection of the retina upon the cerebral cortex but Poljak (25) was the first to demonstrate the precise mosaic arrangement of projection fibers. I have made some measurements of the accuracy of this mosaic in the rat (19). It may be described by the statement that less than one per cent of the cells of the thalamic nuclei have their cortical connections displaced from precise mosaic correspondence by as much as 4 cell diameters. This arrangement could be accounted for by parallel growth of fibers, as suggested by Stoffels' principle of lamellation (29), but the evidence indicates a high degree of neuron specificity in growth. Spatial disarrangement of fibers does not preclude their terminal topographic arrangement. The retinal fibers from different parts of the rat's eye are completely intermingled in the optic nerve but restored to their topographic positions in the optic tract. Sperry's studies (26, 27) of optic nerve regeneration confirm the inference from normal structure. He cut the optic nerves in amphibia and inverted the eyes in the orbits. The optic nerves regenerated and reestablished detail vision. The visual fields of these animals were permanently inverted so that all of their visual reactions were misdirected by 180 degrees. The regenerated fibers were completely intermingled in the scar, yet injuries to the optic lobes showed that each part of the retina had been reconnected with that part of the lobe to which its fibers go when the eye is in normal position. The conclusion seems established that the nerve fibers from every point in the retina are specified for a functional connection with a corresponding point in the optic lobe.

This same precision of projection of sensory surfaces to receptive regions, to the cerebral cortex in mammals, seems to be true for all sensory systems except the auditory, and for all mammals from marsupials to man. It may also be true for efferent paths, although they have not been so carefully studied. The role of heredity in behavior has some-

times been questioned on the ground that complex behavior involves a precision of nervous organization which cannot be attained by gene determination and the processes of growth. The evidence for predetermined specificity which seems to extend even to the growth and connections of individual cells is a conclusive reply to such arguments and sets no limit to the specificity of reaction patterns which may be determined by constitutional factors.

There is no conclusive evidence as to whether this precision of connections is actually continued throughout the circuit which mediates a reaction. Some reflexes may be so integrated, but it is highly probable that the mosaic arrangement is not continued through the cerebral cortex. Anatomic studies of the cortex indicate chiefly a network of short and frequently reflected circuits; physiological studies show diffuse connections. Strychninization of a point in one area, for example, may fire the entire area or the whole of an adjacent area, indicating that every point has widespread, diffuse connections.

The definite afferent and efferent paths provide two basic mechanisms of behavior. On the one hand they result in a segmental arrangement of connections which provides the pattern of reflex organization. The lamellar arrangement of fibers can determine much of the organization of reflexes by producing a segmental distribution of efferents and afferents. In the cortex and in other integrating structures, like the tectum, the topographic representation of sensory surfaces provides a spatial distribution of excitation within which 'field forces,' whatever be their nature, may act.

Little is known of the intrinsic organization of the cortex but its basic structure of multiple laminations and conducting loops of diverse lengths is constant throughout the mammalian series. There are indications that rather complex functions are inherent in this basic structure. Thus the general laws of perceptual organization are the same at all levels of the vertebrate series in which they have been tested. (It is scarcely necessary to point out that the organization of perception is not a property of stimulus energies but is imposed by the nervous system. This fact is especially obvious in visual illusions and in stimulus equivalencies.) Our experiments on isolation of the visual cortex in rat (Lashley, 20) and monkey and on the function of small remnants of the visual cortex (Lashley, 18) indicate that the perceptual organization is intrinsic even within very small bits of a total functional system.

From the detailed specificity of the growth processes and the uniformity of such complex integrations as are implied by the constancy of perceptual organization throughout the mammalian series, we are compelled to recognize that the genetic determination of behavior may extend to very intricate and precise coordinative processes.

INTERSPECIES DIFFERENCES IN NERVOUS STRUCTURE

Superimposed on the basic constancy of structure are species differences in a great number of anatomic characters. Most obvious are differences in the absolute size of the brain, with a range from half a gram in rodents to some 7000 grams in cetacea. Brain volume is only a rough indication of other variables of greater behavioral significance and its relation to such variables is largely unknown. In the motor cortex the cells of the third layer of the cat's brain are larger than those of man although the cat's brain weighs only one fiftieth as much as the human. In the monkey's brain these cells are smaller than in man. In the monkey's visual

cortex the cells are much smaller than in man, except the large stellate cells, which are of equal size (von Bonin, 7, 8). The ratio of cell number to the surface area of the cortex is of the same order in the rat and in man, but the proportionately larger and more densely crowded cells of the rat's brain leave less room for the felt-work of intercellular fibers. There is need for a systematic study of such variables before the significance of quantitative differences in cerebral structure can be interpreted. In general, cell number seems to correlate rather closely with brain size in interspecies relations. Brain weight, or rather the excess of the brain-body weight ratio over the average, represented by Dubois' index of cephalization, shows a fairly close correspondence to behavioral complexity (von Bonin, 6), although the reliability of measures in comparative psychology is so low as to make most comparisons questionable.

Comparative studies of the brain have been largely restricted to easily measured characters which probably have little functional significance. Much has been written about the relative increase in the size of the frontal and other associative regions in primates, as compared with other animals, and of the significance of this development for the intellectual superiority of primates. I am sceptical of these conclusions, for they are based upon measurements of gross divisions of the cortex into lobes which have doubtful boundaries and questionable functional significance. If the comparison is based upon the projection fields of the thalamic nuclei, which provide the best available index of cerebral diversities of function, the quantitative differences in relative sizes of functional fields, even between the rat and monkey, are very greatly reduced. The more significant differences are almost certainly in microscopic organization, rather than in gross dimensions.

Some functional diversities correlating with the size of cortical fields determined by other than gross anatomic methods have been demonstrated. Thus Adrian (1) has shown that in the Shetland pony the sensory projection field for the nostril is as large as that of all the remaining skin surface. In the goat the lips have a corresponding representation. Use of the nostril by the pony and lip region by the goat for tactile exploration corresponds to the extent of sensory projection. In ungulates few pyramidal fibers extend beyond the medulla and the variety of control and modifiability of limb movements is correspondingly reduced. In these cases patterns of behavior are determined by cerebral differences.

Comparative studies of the histology of the cortex have been confined almost entirely to attempts to confirm Brodman's functional divisions and the available data are inadequate for any certain functional correlations. The brains of lower mammals show a closer crowding of cells and a lesser variety of cell forms, which imply fewer and simpler intracortical connections. Some marked differences in structural connections are indicated, though their functional significance is unknown. Thus the lateral geniculate nucleus of the cat contains two types of cells in about equal numbers, only one of which degenerates after removal of the striate cortex. By contrast, all cells of this nucleus degenerate in the rat and in primates after decortication. Equally striking differences in the connections of the medial geniculate occur in various animals. Differences in relative size of thalamic nuclei even between closely related species of primates are especially striking.

A comparison of the cerebral histology of different species of primates shows a wide range of differences. For

example, large Betz cells are distributed throughout the postcentral region of the macaques and are absent from the region in New World monkeys. Various species differ in the complexity of lamination of the visual cortex (von Bonin, 9). Many other differences appear but observations are based on too few individuals to assure that they are consistent species differences.

Differences in the chemical constitution of the brain may be even more significant for behavior than are structural differences. The available techniques are not satisfactory for direct determination of chemical variations. Reliable differences in protein and lipid composition have been found, but it is not certain whether these represent chemical differences in the functional elements or merely differences in proportion of nervous to supporting elements. More significant is the evidence on the effects of hormones. Sex behavior in the males of lower animals is very largely dependent upon the presence of androgens and impotence develops rapidly after castration. In the chimpanzee, on the contrary, early castration does not abolish or even reduce the sex drive. However, the dominance of the chimpanzee in the social group definitely varies with the supply of sex hormone, increasing with androgens and decreasing with estrogens (Clark and Birch, 11). Evidently there are phylogenetic differences in the reactivity of nervous structures to these chemicals. Similar differences in sensitivity to drugs and toxins are indicated, though they have not been systematically studied.

A comparison of mammalian species can do little more at present than enumerate the kinds of structural differences existing between animals which show characteristic differences in behavior. It is rarely possible to relate a specific type of behavior to a definite structure. It might be argued that the structural differences which we observe are immaterial for behavior. However, the species characters are so constant under a variety of environmental conditions that they cannot be ascribed to experience. The macaques and New World monkeys, for example, differ fundamentally in temperament and in behavior patterns, whether they have been trapped and imported or bred and reared in relative isolation in the laboratory. The interspecies differences are certainly genetically determined and structural differences in the nervous system provide the only conceivable basis for the genetic traits.

INDIVIDUAL VARIATION IN NERVOUS STRUCTURE

Except for a few gross characters the study of individual variations in the nervous system has been strangely neglected. There have been innumerable studies of variation in external bodily characters and attempts to correlate the differences with behavior traits. Such studies have included almost every measurable character from cephalic index to width of pelvis, from length of nose to color of hair. But the one organ whose variations might reasonably be expected to produce behavior differences has received almost no attention. The brain is, of course, relatively inaccessible and its study, except for gross differences in dimensions, requires special and laborious techniques, but these facts do not justify the neglect of the problem of central nervous variability. Even the limited material available, however, indicates that individual variation in brain structure within a species is of the same kind and often equal in extent to that between species. Studies of structural variation have been largely limited to primates and heritable variations have been recorded chiefly in cases of deviations which result in distinctly abnor-

mal behavior. The reason for this is that neurologists have been primarily interested in clinical problems and consequently have studied human material. Pathological traits are readily identified and most frequently recorded in family histories. Their heredity is therefore most clearly established. The far more promising field of normal variation in animals has been almost entirely neglected. I shall list some of the more conspicuous individual differences in brain structure that have been observed within species of mammals and discuss briefly their possible significance for behavior and their genetic determination.

Individual differences in human brain weight have been rather extensively studied. Comparison of the brain weights of 100 eminent men with 1334 run-of-the-hospital patients by Spitzka (28) gave an average difference of about 9 per cent heavier for the former. The distribution curves were similar and the range almost the same. Basset (3) found the strain of Wistar rats of deficient brain weight were somewhat deficient in learning ability in comparison with controls which averaged 6.5 per cent higher in brain-body weight ratio. These figures indicate a trend which is not great but is possibly significant. The correlation of brain size with ability is positive but very low. The inheritance of brain size is indicated both by the Wistar rats and by several studies of weight of the brains in human races which have given fairly consistent differences of about 10 per cent between white and East African negro races (Vint, 30).

Further evidence of the heredity of gross brain structure is given by Karplus (17). He compared the patterns of gyri in a number of family groups, chiefly mother and child. He found definite similarities in fissurization, which tended to be ipsilateral; that is, the hemispheres of the same side in relatives tended to be more alike than were the two hemispheres of the same individual. Functional correlations with fissurization have not been demonstrated. I quote from Donaldson (12), "I recall the perplexity of my old friend, Burt Wilder—who was a persistent student of cerebral pattern, and inclined to give value to the form of fissurization —when he found the brain of Chauncey Wright, a distinguished mathematician, so poor in fissurization that it was almost infantile in appearance." Cortical folding may have no behavioral significance. Nevertheless, the genetic similarities in fissurization indicate the extent to which heredity may contribute to the details of brain development.

A few hereditary variations in the size and distribution of tracts within the brain have been reported. Hereditary absence of the corpus callosum occurs in mice and a number of developmental anomolies in the eye and optic tracts of rodents ranging from cyclopia to absence of optic structures have been described as genetically determined (Chase, 10). The same defects appear frequently in man, though their genetic determination has not been established.

In the familial disease, athetosis, in which there are forced movements of the limbs and torsion of the neck and trunk, the corpus striatum contains characteristically a large number of irregular, twisted fibers which give it a marbled appearance; the status marmoratus of Vogt. Alexander (2) has shown that these marblizing fibers represent a part or all of the fibers of the fronto-pontine tract which have been diverted from their normal course. The condition is definitely familial, although its expressivity is low. Karplus (17) has reported histological studies of the medulla in several family groups. Three siblings, a boy of 4 and girls of 5 and 6 years all showed a marked development

of a transverse bundle of fibers in the floor of the fourth ventricle, the superior arcuate bundle. A similar development occurred in less than 10 per cent of other brains studied. These three brains also showed a focus of small cells in the hypoglossal nuclei, surrounded by a dense layer of medullated fibers, a condition found in only one of 30 other brains. In other family groups there were also variations common to all members. Thus even a superficial and incomplete comparison of a few family groups revealed several hereditary structural variants, indicating the frequency with which such genetic differences must occur.

Variations in other microscopic structures of the primate brain are very common though not known to be hereditary. Alexander (2) says of the structure of the thalamus, "The myelo-architectural pattern of the normal thalamus shows a surprising number of individual differences, and in studying them closely, one is led to the conclusion that human thalami are almost as different in appearance as human faces." I can confirm this variability from study of thalami of the cat and monkey.

A number of familial pathological conditions of the nervous system suggest a wide range of hereditary developmental deficiencies, recognized only when they are so extreme as to seriously incapacitate the individual. Marie's cerebellar ataxia with deficiency or absence of Purkinje cells, Friedreich's ataxia with varying spinal deficiencies are examples.

Individual differences in the cortical architecture of man have been studied chiefly in relation to mental deficiency. Hammarberg (16) found a subnormal number of neurons and increased glia throughout the cortex in aments. Bolton (5) reported thinner cortex and sparse cells in the frontal regions of the aments that he studied. Norman (24) and Berry (4), in separate studies, failed to confirm a reduced cell number in mental deficiency but did find a very irregular arrangement of cortical cells, which may indicate abnormalities of fiber distribution. Ellis (14) reported cell deficiencies in the cerebella of mental defectives. These results are in agreement in indicating abnormal architecture in the brains of mental defectives, although they do not indicate a single type.

I have been much impressed by the differences in cell structure of the cerebral cortex which Dr. George Clark and I have found in comparing the brains of a series of spider monkeys, *Ateles geoffroyi* (21). There is a wide range of variation in almost every cytoarchitectural character. Thus, two brains differ by more than 100 per cent in the average size of the neurons in the superior frontal convolution, although no such differences are present in other parts. Differences of more than 25 per cent in the number of cells per unit volume of the cortex of the temporal lobes distinguish two other brains, and local differences of as much as 100 per cent in cell density have been observed in more restricted regions of the frontal lobe, operculum, and parietal region. Betz cells, the large cells characteristic of the precentral gyrus, may occur in some brains in the prefrontal region, in combination with a thick granular layer. In one brain a number of very large cells are present in the third layer of the cortex throughout the opercular region; these cells are more than double the size of any cells found in the same region of other brains. Many localized differences in the arrangement of cells in layers, and so by inference in the distribution of fibers, were also observed. In fact there is scarcely a quantitative histological character which does not vary by 25 to 100 per cent in local regions.

No similar study of the human brain has been made. Von Economo (13) reported differences in cell density of the two temporal lobes of one brain as great as 10 per cent. The differences in the mapping of the cortex by Brodmann, Campbell, the Vogts, and Economo and Koskinas, and in their descriptions of cortical structure, suggest that localized individual variations in the cellular structure of the human brain may be very frequent.

These localized differences in cortical structure within a series of presumably normal specimens are similar to the more wide spread differences that have been held to distinguish normal and mentally defective brains and which, developed to a greater degree, distinguish different species of animals. They are, however, restricted to limited areas of the cortex which are known to have distinct functions. The localized variations therefore offer at least a possibility of individual differences in the specialized functions of the various areas. Knowledge of the specialized functions of cortical areas is derived largely from defects following their destruction. These defects, the various types of agnosia, for example, involve a grouping of functions which has more than chance resemblance to the aggregates which are differentiated as primary abilities by factor analysis. A relation between local variations in structure and the development of primary abilities is clearly suggested by these facts.

Variations in arterial supply of the brain are well known. No structure is more variable than the circle of Willis, and Donaldson (12) has emphasized the possibility that differences in arterial distribution are associated with intelligence level. The behavior disorders produced by temporary disturbances in oxygen level indicate the close dependence of brain functions upon vascular supply.

There are few data on variations in the chemical composition of the brain. The study of developmental changes by MacArthur and Doisey (23) includes analysis of three adult human brains of approximately the same age. The greatest differences are in water content, which is probably very unstable. Allowing for water content, there are, however, differences in protein and lipid fractions which appear to be beyond the error of measurement. Heritable variations in brain chemistry are suggested by some of the degenerative diseases. Amaurotic family idiocy has been definitely related to disturbances in lipid metabolism and involves changes in the structure of the brain as well as of other organs. The familial diseases of late onset affecting the corpus striatum, such as Wilson's disease and paralysis agitans, indicate a special susceptibility of this structure to metabolic disorders which are hereditary, though of low expressivity.

Pedigrees of the heritable pathology of the nervous system follow the pattern of the majority of the heredity traits in mammals. Few mammalian traits appear in the ratios of simple Mendelian dominants or recessives. Perhaps a majority are determined by multiple genes, some of which enhance and others restrict their development. The degree of expression thus varies. One member of a polydactylous race, for example, may have several supernumery digits, another only a small supernumery bud. The recent studies of Lennox and Gibbs (22) present such a condition in a neurological character. The occurrence of irregular brain waves in epileptic families is quite consistent with a simple genetic determination. Convulsive seizures show more sporadic distribution. The character, when present, does not always develop to the ex-

treme required for recognition as major epilepsy.

CONCLUSIONS

The status of the study of variation and inheritance of structure in the central nervous system may be summarized as follows. The brain is extremely variable in every character that has been subjected to measurement. Its diversities of structure within the species are of the same general character as are the differences between related species or even between orders of animals. Some of the structural variations have been shown to correlate with functional disturbances. From what is known of the variations in other systems it may be concluded that the variants which produce pathological symptoms are not discontinuous characters but are the extremes of a normal distribution. Lesser deviations in the same direction, resulting in behavior which is not classed as pathological, are to be expected.

Some of the more conspicuous structural differences have been shown to be hereditary. The heredity of the smaller variants has not been studied and we can only argue their probable genetic determination by analogy with variations in more readily observed structures. Extreme variations like the Hapsburg jaw are conspicuously hereditary and no one can doubt that lesser differences in facial conformation are likewise genetically determined, even though there is more blending and less regularity in their appearance. There can be little question that some of the lesser variants in cerebral structure are likewise hereditary.

Even if this is not the case, if the variants are largely the result of developmental accidents, they still present a serious difficulty for the environmentalist. Discussions of heredity and environment have tended to regard the nervous system, if it is considered at all, as a vaguely remote organ, essentially similar in all individuals and largely moulded by experience. Even the limited evidence at hand, however, shows that individuals start life with brains differing enormously in structure; unlike in number, size, and arrangement of neurons as well as in grosser features. The variations in cells and tracts must have functional significance. It is not conceivable that the inferior frontal convolutions of two brains would function in the same way or with equal effectiveness when one contains only half as many cells as the other; that two parietal association areas should be identical in function when the cells of one are mostly minute granules and of the other large pyramids; that the presence of Betz cells in the prefrontal region is without influence on behavior. Such differences are the rule in the limited material that we have studied.

I will not pretend to a knowledge of the functional significance of such variations but they cannot be disregarded in any consideration of the causes of individual differences in mental traits. The need for further investigation of variations in brain structure is obvious. Except for total weight, the normal range of variation has not been determined for any of the hundreds of measurable elements and structures in the brain. Genetic studies of the nervous system have included no more than a dozen family groups. Our own studies of variability are based on only seven hemispheres. Such investigations are extremely laborious but they are not impossible. They require only endless counting and measurement on well prepared specimens. The correlation of variations with behavior presents much greater difficulties. Yet I believe that the results of such studies will repay the labor. Until they have been made generalizations concerning the relative

significance of constitution and experience will rest upon an insecure basis.

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THE HOARDING INSTINCT

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Introduction

Rather than dealing with some general aspect of the heredity-environment problem, this paper simply tells a story about one kind of behavior—a story of the recent experiments with the hoarding of rats. All of the experiments have been carried out since 1939. Many of them are not published yet, but those who are conducting them have been kind enough to let me see their results in advance and to incorporate them in the story.

Problem. Before getting on with the story, it would be well to state the background of the problem of hoarding. In nearly every culture, whether primitive or modern, people spend a good deal of time acquiring things—food, fuel, building material, socially valuable objects. Much of this acquisitive behavior makes good sense; it prepares for some big project like building a house. It prepares for the day when food may be scarce or when things will be needed which are plentiful when they are acquired. Because hoarding often makes sense, we may be tempted to think of it as rational behavior which man has learned to adapt to the ups and downs of life.

But if we look a bit longer at the phenomenon, we see that hoarding often goes beyond the bounds of reason. Men sometimes spend their lives accumulating vast hoards of wealth and property which they can never use. Some simply collect more or less useless objects—jewelry, antiques, glassware, stamps, and the like. Such hoarding beyond the necessities of life occurs not only in modern technological societies but also in primitive peoples. Certain tribes in the South Sea Islands, for example, who live in fertile lowlands where food is abundant, are dominated by a desire to collect large stores of food. So it is not quite obvious that hoarding behavior is a purely rational matter. It is hard to tell just what human hoarding is.

As psychologists we have learned to carry many problems from the realm of human behavior, where they are difficult to solve scientifically, over to animal behavior where we can control our experiments more carefully. The results do not always give us a direct answer to the problems of human behavior, but they give us good hints or fruitful ideas for human research. So it has been with hoarding behavior.

Many animals, as you know, also hoard. Nearly everyone has seen the common squirrel busily engaged in collecting and burying food. The pack-rat is famous for his exploits in carrying and hoarding various objects. The European hamster accumulates such vast hoards of grain that, in times of famine in Europe, his hoards have been raided to supply human food. These are but a few examples of animal hoarding.

If hoarding is so universal that it occurs frequently not only in man but lower animals as well, it would look as though the behavior might be instinctive—for universality of behavior has come to be one of the criteria for establishing the innate, rather than the learned, character of behavior patterns. It is clear, on the other hand, that some aspects of hoarding in man must be learned, for the desire to hoard money, for example, which has no direct bio-

logical value, must be learned in some way. Thus we come to an interesting problem in the roles of heredity and environment. Is hoarding behavior instinctive or acquired? Perhaps it is both. If so, what aspects of it are instinctive and what are learned? That is the question for this paper.

Method. To attack this problem, we need a convenient subject—one which will do what we want when we want it, so that we can carefully control the many factors which may enter into the problem. As usual, the common laboratory rat stands us in good stead. In addition to his many talents which have been exploited for years, he also hoards. Wolfe (17) first showed that he does in 1939, and he demonstrated, as well, that hoarding in the rat could be produced and studied scientifically. A short while later, Hunt (1) devised an apparatus which has become more or less the standard for hoarding studies. The apparatus consists simply of an alley, about eight inches high and wide and about three feet long. At one end of it is a bin full of pellets of food; at the other end is the rat's home cage, where the rat ordinarily eats, drinks and sleeps. With an apparatus of this sort, more than a score of experiments have been carried out in the last eight years.

Most of the experiments have been with food-hoarding; in fact, all of those published to date. To be published shortly, however, is an ingenious study by Bindra of water-hoarding in the rat. To get that, Bindra soaked dentist's pledgets with water, thus making water-pellets. It is too early to give you any details on water-hoarding except to say that it can be gotten. The rest of the experiments which I shall describe are with the hoarding of pellets of food.

IS HOARDING INSTINCTIVE?

The big question for this paper, as I said above, is whether hoarding is instinctive or acquired. That, of course, is a black-and-white question, and it would be dangerous to give a simple "yes" or "no" to it. The truth is usually complicated and this case is no exception, but it is simple enough to make a straight-forward story. Here it is.

Innate or acquired. This we can say, that it takes no teaching or conditioning to get a rat to hoard. In dozens of experiments by different people, all that is necessary to observe hoarding is to put a rat in a hoarding apparatus and give it sufficient opportunity (1, 5, 9, 13). Adult rats, fully watered and fed, will hoard five to twenty pellets per day if placed in hoarding apparatus and left there (5). Since the rat only eats one or two pellets a day, this is plainly hoarding. And since it comes out spontaneously without training, it is plainly instinctive. Of course, rats may have learned to hoard early in infancy because of competition for food in their home cages, but hoarding is so universal in laboratory rats, always fully fed and watered, that such learning is extremely unlikely.

Emotional adaptation. But before we jump to conclusions, let me hasten to point out that there is some kind of adaptation, although it is not to be called learning, that is involved in hoarding. The hoarding which eventually appears is usually not seen in the first few minutes a rat is placed in the hoarding apparatus. If a rat is allowed only thirty minutes a day in the apparatus, it may be several days before appreciable hoarding takes place. Moreover, other things being equal, animals which have had an opportunity to become familiar with the hoarding apparatus before hoarding trials are begun will hoard more readily than those which do not. We may infer from these results that emotional responses to an unfamiliar situation may interfere somewhat with hoarding and that emotional

adaptation assists hoarding behavior. Such emotional adaptation, however, is neither learning nor a primary factor in hoarding behavior.

WHAT CAUSES HOARDING?

If hoarding is an innate instinctive mechanism, what then is the cause of it? When we speak of causes, of course, we must always make a distinction between necessary and sufficient conditions, that is, between factors which must be present for something to occur at all and factors which help it occur or augment the size of its occurrence. Thus, we must ask two questions. What is essential to bringing out the pattern of hoarding behavior? And, secondly, what facilitates hoarding, or determines the form and amount of hoarding, once it has been elicited? The remainder of this paper will tell what we have learned thus far about these two questions.

Temperature. First consider the question of what instigates hoarding behavior in laboratory rats. For one thing, we know that low environmental temperatures will instigate hoarding (5). There is, in fact, a rather nice mathematical relationship between hoarding and environmental temperature in which the logarithm of pellets hoarded is inversely proportional to the environmental temperature. This fact is based on experiments in which rats were left continuously in the hoarding apparatus for several weeks, amply supplied with food and water, while the temperature of the room was varied from day to day between summer and winter temperatures.

Thus, low environmental temperature is one factor inducing hoarding. And it is interesting to note that this instinctive hoarding response to low temperature is a very useful mechanism in the normal wild life of the animal, because food ordinarily becomes very scarce in the cold seasons of the year. Instinctive hoarding, as the temperature grows colder, provides the animal with a mechanism for storing up food at just the time of year when such a store will be needed most.

Food-deprivation. Another important factor in inducing hoarding is food-deprivation. Such food-deprivation, in fact, is the surest way to get the most hoarding in rats. Nearly all of the experiments done to date have employed food-deprivation as the means of inducing hoarding. The usual procedure is to place rats on twenty-four hour hunger cycles in which no food is available for twenty-three hours and only one hour each day is allowed for eating and hoarding. After a few days on such a schedule, rats will hoard as many pellets in one half-hour's test as will fully-fed animals in twenty-four hours at low temperatures (11). If one then discontinues the deprivation cycle, putting the animals on a continuous, ample supply of food, the amount of hoarding remains high for about twenty-four hours and then declines over a period of three or four days, sinking finally back toward zero, as the rats become more and more satiated. The effects of food-deprivation on hoarding have now been studied in considerable detail, and there are many fine points which one might review. Suffice it to say here, however, that food deprivation is, so far as we know at present, the most important single factor in instigating hoarding behavior in laboratory rats.

Physiological factors. The importance of environmental temperature and food-deprivation in inducing hoarding behavior raises some interesting questions concerning the physiological basis of hoarding. Both low temperature and food-deprivation deplete an animal's store of food materials in his body, especially the types of material such as sugar and glycogen which are used by the body as relatively short-term sources of energy. Unfortunately, however,

practically nothing is known of the physiological factors which may be the immediate cause of hoarding. One preliminary experiment (13), raising more problems than it settles, has been done with the injection of glucose, insulin, and adrenalin. Yet to be done, however, are experiments which will tell us whether some factor, such as metabolic rate, depletion of the body's sugar reserves or other biochemical factors, is basic to hoarding. We yet know nothing, moreover, concerning the neural mechanisms of the 'hoarding instinct.'

WHAT INCREASES HOARDING?

Infant-deprivation. We may next turn to a consideration of the factors which facilitate hoarding and are of secondary importance in it. One of the most interesting possibilities is that extreme deprivation at one point in the animal's life, particularly early in infancy, may thereafter predispose it to hoarding, even though there has been little or no deprivation in the meantime (1). Psychoanalysts have stressed the idea that the frustration of primary drives, such as feeding and suckling in infancy, may be at the root of greediness and acquisitive patterns of behavior in adult personality. Again, in the hoarding behavior of some primitive tribes which have abundant food, there is the suggestion that these peoples regularly experience food-deprivation when they are nursing in infancy and that this factor may be responsible for the hoarding habits which characterize the adult group.

This suggestion has been put to a test with laboratory rats (1, 12). Young rats were taken shortly after weaning (twenty-four days of age) and put on a rather severe schedule of deprivation for a period of eight days. They were then placed on a normal adequate diet and allowed to grow up to adulthood. At that time they were compared in hoarding tests with litter mates who had not experienced such food-deprivation in infancy.

No effect at all appeared when the rats were given brief hoarding tests while being completely satiated, but the rats deprived in infancy hoarded significantly more when placed on a twenty-four hour deprivation cycle than animals which had had no infant-deprivation. Thus, the effects of infant-deprivation on hoarding could be seen in adult animals subjected to some deprivation. More extensive research is now in progress in which the infant-deprivation is being carried out at an earlier age when rats are nursing, but it is too early yet to report the results (2).

Constitutional factors. There is a suggestion—but only a suggestion—that some rats are constitutionally more prone than others to hoard food. In an analysis of effects of infant food-deprivation on hoarding, Hunt (2) finds that some litters are significantly affected by the deprivation when others are not. Whether this litter-factor comes from differences in nursing care or whether it is a constitutional factor present at birth and/or having a genetic linkage remains to be determined. Experiments, which have just begun in the Johns Hopkins laboratory, in the selective breeding of hoarders and non-hoarders might settle this question.

Frustration. Next we may turn to the factor of frustration. This has been distinguished from deprivation by some of those working in the field (3, 6). They use deprivation to refer to giving the rat considerably less food than he will ordinarily eat if he has the opportunity; and by frustration they refer to thwarting an animal in his attempts to obtain food placed where he can see it, smell it, or touch it. It is rather difficult, however, in the case of hoarding

behavior, to set up experimental procedures which will clearly distinguish between the effects of deprivation and frustration. In one experiment (3) frustration consisted simply of taking some food away from animals before they had the opportunity to eat it. This experiment showed no effect of frustration on hoarding. Another technique, however, used by another investigator (6), showed clearly that frustration, added to deprivation, significantly increased the hoarding induced by deprivation. His technique was to frustrate animals by placing pellets of food in a little wire enclosure inside the cage while the animal was hungry. Thus, the food was clearly visible to the animal, in fact almost within its grasp, but all attempts to obtain it were thwarted. Animals frustrated in this way hoarded nearly twice as many pellets, when given hoarding tests, than controlled groups subjected to the same amount of deprivation without such frustration.

At this point we may stop a moment to take stock. We have seen that hoarding is not learned, but instinctive. It is induced by low temperatures and by food-deprivation. Once induced by such factors, hoarding is further increased by past experience of food-deprivation and by psychological frustration. That, in brief, is what we know about the factors arousing or strengthening the hoarding instinct, and it is rather sketchy. Several years more of research should give us a more detailed and systematic account of the mechanism of the 'hoarding instinct.'

WHAT IS HOARDING BEHAVIOR?

There are, however, several other interesting questions concerning hoarding which we have not considered. It is not enough to say that hoarding is instinctive, that it has a physiological basis, and that it may be affected by frustration. We may also ask just what hoarding is, what objects are hoarded, and where they are taken to.

The goal of hoarding. What, first of all, is the goal of hoarding behavior? Is it to accumulate a particular number of pellets? Does the animal stop hoarding when he has accumulated a pile which he 'thinks' will satisfy his future needs? Or is it an expressive activity arising from an 'urge,' which never reaches a particular goal? To these questions of the goal of hoarding, we have a definite answer (7, 11). In two different experiments, the hoards of pellets accumulated by animals were stolen from them at some time in the hoarding tests, to see whether it would affect the number of pellets hoarded during the remainder of the test. Presumably an animal would hoard more when its hoard was taken from it, if the rat's goal is to achieve some pile of pellets. In no case, however, did it make any difference. We may conclude, therefore, that the rat hoards just to hoard, and that it does not care whether it keeps what it hoards or whether it achieves any particular goal. The amount of hoarding seems to depend on an 'urge' to hoard rather than on how much hoarding has actually been accomplished.

Object of hoarding. Another interesting question is, what is the object of hoarding? Will the rat carry anything to the home cage or is it so discriminating as to select only food? To this question there is not such a clear answer. In one unpublished experiment with animals being maintained on a twenty-four hour deprivation cycle and tested daily (Johnson), blocks of wood, of about the same size as the pellets ordinarily hoarded, were substituted in the hoarding bins. No hoarding took place. In a few cases the rats carried a piece or two of wood back to the home cage, but not enough to be called

hoarding. Thus, in food-deprivation, rats select food as the object of hoarding, not some imitation. It would be interesting to carry the experiment further to study what aspects of the food-pellets make the rats select them for hoarding.

Home. Another question is to what place the rat hoards. In most of our experiments, the cages in which the rats ordinarily live are simply moved up to the hoarding alley and the animals carry pellets from the bin at the end of the alley to these cages. But what makes a home cage? In experiments to get at this question (16), strange cages, either clean or previously inhabited by another animal, were interchanged with the familiar home cage in which a particular rat had been living. The effect was clear-cut; the rats would not hoard to a strange cage. Instead, they would carry the pellets toward the cage, as they were accustomed to do, but would leave them regularly in the alley outside the door. To see what factors so clearly distinguish the strange cage from the familiar home cage, further experiments were conducted in which the olfactory and visual cues of the home cage were separated (9). Some hoarding would occur when the cage either looked like or smelled like the animal's regular home cage, but of these two factors, odor was the more important. Thus, in brief, we may say that the rat hoards, not to some strange place, but to a familiar home cage and that it is the familiar odor which makes the cage seem most like home.

Light and dark. There is another phenomenon, not yet too well understood, of the effect of light on hoarding to a home cage (12). If lights are placed over the rats' home cages, hoarding induced by food-deprivation is sharply depressed. Indeed, the effect is much like that of substituting a strange cage for the familiar home cage. This fact fits together with our knowledge from other experiments (4) that rats do not like light and generally tend to avoid it. Apparently the home cage is not nearly so much like home when it is lighted as when it is darkened, and the rat hoards correspondingly less.

Also of interest is the effect of lighting alleys on hoarding (12). This, surprisingly enough, increases hoarding, other things being equal, by a factor of 2.5 times (12, Fig. 6). The great increase in hoarding from the lighting of alleys will persist, moreover, for days afterward when the alleys are again darkened. It is difficult at present to interpret this fact. Perhaps alley-lighting sharpens the contrast between the outside world and the home cage. Perhaps the undesirable lighting increases the emotion and anxiety of the rat and this in turn increases hoarding. Only further experiments can tell us what to make of the phenomenon.

Social competition. Finally, we note briefly the interesting question whether hoarding behavior may be affected significantly by social competition. It is conceivable that rats which would otherwise not display hoarding behavior might do so when placed in competition with other rats for food. There are no conclusive data on this question, and it could be the subject for some interesting researches in the future. We have only one preliminary experiment (8) in which four rats were allowed to hoard simultaneously from a central bin to their respective cages. In this situation, some animals hoard to their own cages from the central bin as they do when hoarding in isolation, but some animals ignore the central bin and insist on stealing pellets from the hoard collected by another animal in his home cage. It is only in this way, so far as we know at present, that hoarding behavior may be socially conditioned by competitive situations.

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METHODOLOGICAL RESOURCES FOR THE EXPERIMENTAL STUDY OF INNATE BEHAVIOR AS RELATED TO ENVIRONMENTAL FACTORS

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The principal methodological resources available for experiments on innate behavior in animals, as related to environmental influences, may be listed under four general headings: (1) The method of uniform heredity and varied environment; (2) The method of uniform environment and varied heredity; (3) The method of genetic analysis; and (4) The method of cytological analysis.

The object of each of these is to discover fundamental principles by which one may account for the diversity in behavior systems of animals about us. This diversity embraces not only the grosser dissimilarities obtaining between species, but also the finer differences occurring among individuals of a single species. They are logical developments from certain broad generalizations that were implicit in the minds of prescientific students of animal behavior, namely, that

(1) Every natural habitat contains natural groupings of animals which are standardized, so to speak, for life in that habitat as judged by their behavior systems relating to alimentation, defense, aggression, reproductive processes, etc.;

(2) Variants of these natural groupings are widely distributed on the earth, where habitats differ in specific details, such as length of seasons, amount of rainfall, prevailing plant and animal life, etc.; and

(3) Highly significant relationships are constantly recurring from generation to generation between elemental details of behavior systems and specific features of these varying habitats.

Fanciers and practical animal breeders may have taken into account the facts on which these generalizations rest when establishing the chief races of domestic animals which have come down to us from primitive times. They brought together typical representatives of these natural groups. By testing them side by side, under similar conditions, they gradually determined which best measured up to their crude standards for growth, docility, fecundity, and other characteristics which struck their fancies or appealed to their sense of economic values. These pioneers observed which representatives maintained their distinctive features in new habitats and flourished in competition with the local breeds which had long since become standardized for that region. Details of behavior which appeared or disappeared quickly when representatives were taken to new habitats were tentatively regarded as reversible modifications; whereas, characters persisting through successive generations in the new habitat were tentatively ascribed to hereditary makeup. These principles and practices shed whatever light the early naturalists and primitive husbandmen had regarding modifications in animals with uniform heredity, as opposed to variations denoting basic differences in hereditary constitution.

Let us now consider a few examples in which these four methodological resources already have played or could play significant roles in nature-nurture research.

THE METHOD OF UNIFORM HEREDITY AND VARIED ENVIRONMENT

The unit of primary importance in investigations of the effects of varied environment on uniform heredity is the individual. By way of exemplifying this, one may cite uses to which clones of unicellular organisms are put. Individuals of a clone are the product of uniparental reproduction. All have the same heredity and, being as numerous as anyone might desire and capable of reproducing over long periods of time, they are extraordinarily favorable for fundamental studies wherein heredity is held constant and environment varied. When reared in pure culture, they are completely free of contaminating bacteria or other microorganisms whose presence might lead to equivocation in the interpretation of changes effected through environmental manipulations. Thus behavioral variations in representatives of one clone express in very high degree the direct cause and effect relationships obtaining between stimulus and protozoan as opposed to indirect relationships secondarily obtained through contaminating organisms. Clones from more than a hundred varieties of protozoa in pure culture are now being used in nature-nurture research relating to motor adjustments to tactual, thermal, luminous, electric, chemical, or other stimuli; to likeness and difference in appetitional behavior; to mass behavior, regarded as a population problem; to alterations in behavior associated with somatic and physiological acclimatization to favorable and unfavorable experimental conditions, *i.e.*, to *Dauermodifikationen* as the German scientists call them; and, finally, to studies of age cycles, characterized by Jennings as sexual immaturity and maturity, wherein one encounters the social phenomenon of conjugation. On this topic Jennings (1) reports that in *paramecium bursaria* there is one variety which has four distinct mating types; a second variety with four more mating types; and still a third with eight additional types. If one lets the letters A, B, C, and D denote the four conjugal types in variety one, one may expect to encounter just six kinds of pairings: namely, AB, AC, AD, BC, BD, and CD. Representatives of one type will mate with representatives of any of the others, but never with those of its own. Even when all sixteen of the mating types from the three varieties are put together there is an unerring assortment of matings according to the aforementioned principle. Extensive use of the clone under conditions in which many details of environment were varied systematically greatly facilitated the discovery of this primitive forerunner of sexual dierotism.

The propagation of individuals from cuttings is another useful device for holding heredity constant while varying environmental influences. Using cuttings from planaria, Child (2) and others working in the field of agamic embryology were able to determine with great precision how specific environmental agencies influence the development of the embryo at all stages of growth and behavioral individuation. The use of cuttings from animals in nature-nurture studies is analagous to the use of cuttings in plant culture when it is necessary that the factor of heredity be held constant while environment is systematically varied.

Polyembryology also affords an opportunity for the use of uniparental stock. With this phenomenon, or something akin to it, we are already familiar in human psychology because it involves the development of two or more offspring from one ovum. In the rat, uniovular twins can be produced experimentally and transplanted from one to another host of the same species as

needed to vary the environment; in certain respects also, young armadillos, the behavior of which has not been studied intensively, regularly emerge as quadruplets from one ovum. Thus, each mating provides four individuals with uniform heredity for nature-nurture researches. But still more striking is polyembryology in many species of the parasitic insects (3). Here the number of individuals developing from one egg may reach 2000 or more. Both haploid (male) and diploid (female) offspring result from this mode of reproduction and a single brood may contain both sexes in varying number. Since the hosts of some of these can be cultured under laboratory conditions they should be excellent subjects for systematic studies of behavior in offspring with identical heredity and varied environment. As yet, however, advantages of parasitic insects for behavioral research have not been recognized by comparative psychologists. That they may be of paramount importance, nevertheless, is evidenced by the fact that they constitute one of the most effective controls of other insect pests which prey upon our most valuable agricultural crops. Hence any fundamental behavioral discoveries made may be of invaluable usefulness in the broader field of applied entomology.

Still another area rich in opportunities for the application of 'method one' would involve greater use of highly inbred strains of animals which are now available in quantity lots. With homozygous insects, birds, mice, rats, guinea pigs, and dogs, one might study the behavior systems involved in alimentation, fecundation, parental care, defense and aggression, thermal regulation, etc., under conditions of varied environments with great profit to the science of psychobiology. One may vary the natural habitats—using, for example, a maritime region in contrast with an arid region of similar latitude and elevation, or sea level as opposed to alpine elevations; also, one may use the experimental laboratory in which the more essential factors of the internal as well as the external environment are varied one at a time or in such combinations as desired. Ultimately, however, the natural setting is required to test the all-round harmonious working of all action systems of the organism. To many of us who have worked for a long time in the field of comparative psychology it is a matter of shame and regret that only an amateurish beginning has yet been made by psychologists in the utilization of pure lines of animals in fundamental research in the nature-nurture area.

THE METHOD OF UNIFORM HABITAT AND VARIED HEREDITY

As in the foregoing method one must decide on the behavior systems to be studied in each run of an experiment. Now the habitat is standardized. This measure must take into account all factors such as food, water, heat, moisture, humidity, radiation, age, behavioral experiences, social stimuli, etc., which are likely to produce modifications in animals with uniform heredity. Into this uniform habitat are brought diverse experimental subjects which have been standardized in nature for different habitats, or those which through selective breeding have come to have stable differences in behavior. Broadly speaking the problem is to determine the ways and degrees to which animals of diverse heredity undergo modifications of behavior under the conditions obtaining in the standardized environment.

This method has been widely used to compare behavioral adaptations in echotypes of *Drosophila* and other insects which are standardized in nature for life in different regions or which have appeared as mutants under lab-

oratory conditions. More loosely speaking it was used at the University of California in a field study of differences in migratory date and nidification of closely related song sparrows which winter near Berkeley but migrate to Friday Harbor in the spring. One of these leaves the Berkeley habitat about two weeks earlier than the other. Its breeding activities (including fecundation, nesting, and brooding of young) are about a fortnight earlier than those of the other. At Friday Harbor the late-comer presents a characteristic difference in nidification. The mother is ready to lay a second clutch of eggs before her first brood has left the nest. She solves this problem by building a second nest nearby and laying the eggs while the mate continues to brood and feed the first clutch until it is ready to leave the nest. In contrast, the echotype which migrated two weeks earlier has a complete clearance between first and second broods. An examination of the early migrants while in the Berkeley region shows that their gonads were activated slightly earlier than those of the late migratory race.

'Method two' is used in practical production tests of laying hens. After standardizing the habitat in a given region, the different breeds of chickens are studied comparatively with respect to many behavioral factors, such as age of onset of laying, amount of winter laying, frequency and duration of broodiness, food preferences, aggressive behavior, etc. All of these behavioral traits have some positive or negative commercial significance.

Also one may recall the behavior studies of Stockard on different pure breeds of dogs. In certain experiments the environment of the experimental laboratory was standardized so as to afford an opportunity for comparative studies of the behavior of diverse genetic types. In the report of Stockard's work there are many items which demonstrate the fruitfulness of the experiments already completed or suggest the desirability of further behavioral studies on dogs of different breeds. Fortunately these may now be undertaken at the Hamilton Station, Bar Harbor, Maine.

Finally I may suggest that there are unrealized advantages to be gained through more extensive use of egg-transplants in mammals. Within a given species one maternal host provides a relatively uniform external environment for genetically diverse embryos and fetuses while they are getting their start. Here again extensive use of inbred strains, wherein the range of phenotypical variation is greatly narrowed, should reveal the genetic background of many behavioral differences. And correlation of these with other characteristic differences may offer clues as to their causation. Some characters needing investigation relate to the phenomenon of hybrid vigor (heterosis) as displayed in animal behavior, appetitional behavior as related to growth, aggressive behavior in social situations, and alterations of behavior with aging, particularly in the period of puberty and senescence.

THE METHOD OF GENETIC ANALYSIS

This is a relatively direct method of studying the heredity of behavioral traits in animals. It involves crossing closely related interfertile echotypes or echospecies and studying the resulting effects of recombination of their genes. Effects of crossing are studied in first, second, and later generations to determine the degree of segregation of the genes in these crosses, and, indirectly, to measure the degree of harmonious working of the genes as evidenced by the ability of the offspring to survive, to develop rapidly or slowly, to compete with others, and to produce nor-

mal offspring. This method makes possible an approximate analysis of the genetic systems of related echotypes and echospecies.

In 1902 Darbyshire (4) demonstrated that the Mendelian principles could be applied to the waltzing character of Japanese mice. This type of activity is not learned by imitation or through tuition or practice. Darbyshire crossed pure-line waltzers with pure-line European albinos that were free from the whirling tendency. All of the F_1 generation, the number running into the hundreds, were free from the waltzing behavior. The first generation hybrids when crossed *inter se* gave ratios of four normal to one waltzer which is a bit off the ratio that would be appropriate if waltzing is transmitted as a recessive unit character; subsequent studies made the latter assumption fully tenable. Historically, Darbyshire's study was significant for pointing out that the determinant of one type of locomotion is transmitted in a standardized environment from one to another generation in ratios similar to those of certain morphological characters.

Other striking instances of genetic analysis involve crosses of domestic hens for the purpose of determining how broodiness is transmitted from generation to generation. Hurst (5), by crossing a pure-line Cochin with a pure-line Black Hamburgh, demonstrated that broodiness is transmitted as a dominant unit character. Also, the tests of age of onset of laying give similar results. Time does not permit of additional special citations, but I may say with confidence that cooperative studies in the fields of genetics and comparative psychology, wherein the method of varied heredity on uniform environment is utilized, will greatly advance our understanding of the combined nurture-nature influences that produce the diversities in behavior within well-known species about us.

THE METHOD OF CYTOLOGICAL ANALYSIS

In its simplest form this method consists of counting the chromosomes of various races or populations under consideration. In the case of insects, we regularly encounter the condition of haploidy. For example, the drone of the honey bee is haploid whereas queens and workers are diploid. In insects one also encounters the condition of polyploidy. As yet, however, the full extent of the behavioral differences, excepting reproductive behavior, between diploids, triploids, tetraploids, and other polyploids have rarely and only superficially been investigated.

In the case of vertebrates, the condition of haploidy is exceedingly rare, but polyploidy is well known. Triploidy is easily brought about in amphibians. Their offspring are viable and capable of living in vivaria under laboratory conditions. So far, however, but few noteworthy behavioral constants associated with triploidy have been cited in amphibians but studies as yet are few and unsystematic. This field is especially deserving of study because the triploids have a smaller number of brain cells than the diploids and their cells are much larger in size. What resultant differences in behavior may be associated with these large nerve cells is a question still open for study.

COMBINED USE OF THE FOUR METHODS

At the outset an experimenter is likely to emphasize but one or two of the foregoing methodological resources.

Ultimately, however, all four have to be employed on the same species because the combined results are certain to provide the truest picture of the growth and motivation of behavior as conditioned by concurrent environmen-

tal and hereditary influences. Together they should reveal how stable behavioral characters are dependent on genetic constitution and how environmental influences fructify what is genetically potential.

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SUMMARY COMMENTS ON THE HEREDITY–ENVIRONMENT SYMPOSIUM

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It will come as a surprise to many psychologists that all five of the distinguished contributors to this Symposium have emphasized the role of heredity in the determination of behavior. Not one has insisted that environmental factors are of primary significance in shaping the psychological characteristics of the individual. I am sure that all of them acknowledge the importance for behavior of the environmental factor whether it is called learning, practice, or the modification of the internal milieu. Historically, the interesting thing is that all of the speakers place their stress on heredity.

Twenty-five years ago, the situation was quite different. Such writers as J. B. Watson and Z. Y. Kuo were conducting a great offensive against the accepted belief that inherited patterns of behavior existed in man and animals. Kuo (1924) entitled one of his papers 'A psychology without heredity' (4) and proceeded essentially to deny even reflexes as inherited patterns of response. Watson (1914 and 1919) originally made much use of the concept of instinct in his books on *Behavior* (7) and *Psychology from the Standpoint of a Behaviorist* (8). However, in the 1924 volume entitled *Behaviorism*, after listing such responses as love, rage, fear, sneezing, feeding, and sex, which were termed unlearned behavior, Watson continues as follows: "In this relatively simple list of human responses there is none corresponding to what is called an 'instinct' by present-day psychologists and biologists. There are then for us no instincts—we no longer need the term in psychology. Everything we have been in the habit of calling an 'instinct' today is a result largely of training—belongs to man's *learned behavior*. As a corollary from this we draw the conclusion that there is no such thing as an inheritance of *capacity, talent, temperament, mental constitution* and *characteristics*" (9, p. 94).

The anti-instinct movement came not only from some of the behaviorists but also from numerous writers on social psychology like Bernard, Dunlap, Faris, and Kantor. I believe that a prime basis for the origin of this anti-heredity movement was the violent reaction against the presentation of the topic of instinct in William McDougall's (1908) *Introduction to Social Psychology* (5). This book reached at least the 22nd revised edition (1931), and few psychologists whose professional careers occupy only the last twenty years have any appreciation of the tremendous influence exercised earlier by this work. The primary instincts and emotions as well as the innate tendencies there described, however, offered a too facile means of describing social behavior, and thus they were wide-open to the type of attack later made on them by the critics. Nevertheless, I should like partly to counteract the neglect from which McDougall's psychology currently suffers by giving a brief quotation from the *Social Psychology* bearing principally on human behavior: "Now, the afferent or receptive part and the efferent or motor part [of the instinct] are capable of being greatly modified, independently of one another and of the central part, in the course of the life history of

the individual; while the central part persists throughout life as the essential unchanging nucleus of the disposition." ". . . the actual bodily movements by which the instinctive process achieves its end may be complicated to an indefinitely great extent; while the emotional excitement, with the accompanying nervous activities of the central part of the disposition, is the only part of the total instinctive process that retains its specific character and remains common to all individuals and all situations in which the instinct is excited" (5, pp. 33–34). That I agree with the gist of these quotations will be apparent in the concluding sentences of this discussion.

The net result of the anti-instinct movement was to all but purge the term instinct from the psychological vocabulary. And it will have been noted that the term is not conspicuous in the present Symposium. Articles on instinct which appeared during the period, for example my own paper in 1920 on 'The modification of instinct from the standpoint of social psychology' (2), received far less attention and exercised for less influence than should have been the case! And writers whose experiments, I think, justified a clear-cut conclusion on the influence of hereditary factors on behavior, for example Leonard Carmichael's article in 1926 on 'The development of behavior in vertebrates experimentally removed from the influence of external stimulation' (1), were led to minimize such an influence.

One should not assume from the foregoing that there have been no excellent studies of instincts and inherited capacities during the past twenty-five years. The contrary is the case. The following are a few examples of such studies, many of them conducted by members of this Symposium: (1) studies of the pecking behavior of chicks; (2) hoarding and maternal behavior of rats; (3) the neurological and hormonal factors controlling emotional behavior; (4) patterns of sexual behavior; (5) the establishment by selective breeding of strains of bright and dull rats; (6) co-twin and race studies of intelligence; (7) unlearned pattern organization of the afferent neural centers; (8) fetal and neonate behavior; and (9) the study of tropisms.

The type of investigation which is conspicuously missing from the above list is the one dealing with the genetics of behavior crosses, work of the character published by Yerkes (10) as far back as 1913 on the inheritance of savageness and wildness in rats. Although the biologist does not limit his discussion of heredity to those cases where the genetics of the transmission of traits has been worked out, it is clear that the understanding of heredity in general rests largely on the experiments in breeding various genetic strains. There is a great dearth of material on the genetics of behavior patterns; and, so far as I can find, no one has brought together in critical summary such studies as do exist.

It is true that there are many genealogical studies of human behavior and behavior capacities, but by and large these do not inspire confidence in the critically minded student unless they deal with the inheritance of such characteristics as color blindness where training and social factors can have but little influence. By contrast the genealogical evidence presented for the inheritance of feeblemindedness, behavior disorders, musical talent, and general eminence is far from convincing support for the conclusion that these aspects of human nature are essentially gene determined. Educational influences, social ostracisms and rewards, and intra-familial relationships may well be the prime factors producing a run of such traits in specific families.

The late Charles R. Stockard in his *Genetic and Endocrine Basis for Differences in Form and Behavior* (6) contributed extensively to the problem of genetics in various breeds of dogs. This work was oriented primarily toward the inheritance of endocrine structure and function and gave little attention to patterns of behavior not hormonally controlled. The results showed typical variations in the histological structure of the glands and typical ratios of glandular to bodily weight for the various dog hybrids. Associated with these variations in endocrine function went certain emotional or temperamental dispositions in the standard dog breeds and in their hybrids. W. T. James and O. D. Anderson, working at the Cornell Dog Farm on Stockard's animals, were able to show the influence of these temperamental traits on conditioning. Anderson comments on the work in part as follows: "The inherited pattern of the internal secretions may differ but slightly between one 'normal' individual and another and, consequently, behavior may deviate but little from one to the other. But when the pattern is a markedly distorted one, the individual's behavior may show correspondingly great deviation from the normal. The glands may thus be found to play a significant role, not only in the production of the various 'normal' types and patterns of behavior, but also in the production of the abnormal types" (6, p. 747).

If it is correct, as it is customary, to say that by behavior we mean motor and glandular responses, then we can say that there is evidence from genetics for the inheritance of glandular behavior. Endocrine secretions are well known for their effects upon brain functioning, as in cretinism, as well as upon the growth and functioning of many other organs. To the extent that the degree of endocrine activity is gene determined, to that extent the genes may be said to determine the above mentioned functions. There is a growing body of evidence which also indicates that one function of the hormones is to sensitize neural centers and thus to make possible the arousal of rare or unsuspected patterns of motor behavior. Drs. Stone and Beach have both contributed to the study of this problem in the field of sex behavior. It is well known even to the lay observer that in many species an individual of either sex may manifest a partial pattern of the sex behavior of the other even without any abnormality of the gonads, although males predominantly exhibit male reactions and females, female reactions. Dr. Beach in particular has clarified this problem in his studies of mating behavior in pre-pubertally castrated male and female rats. Thus he finds that females treated with testosterone show a very greatly increased percentage of essentially completed male sex responses. The total picture is very complex; but the important points to make in the present context are: (1) patterns of sex behavior do appear in essentially unlearned form and in a style typical of the species; (2) the degree of hormonal activity itself may be a gene determined trait; and (3) the existence of male and female behavior patterns in the same individual may be shown or their occasional appearance accentuated by the action of hormones probably acting as sensitizers of neural centers.

I believe that it is important in considering the role of heredity in the determination of behavior to distinguish between direct and indirect effects—between the inheritance of receptors, effectors, or other organs which may indirectly affect behavior on the one hand and the inheritance of those neural patterns which directly control behavior on the other hand. Thus there is no ques-

tion but that human behavior may be different from what it would otherwise be if the individual has hereditary color blindness, or polydactyly, or dwarfism, or even red hair. However, it is not so clear, due to the lack of data on the genetics of behavior crosses, that there are even in animals inherited patterns of neural activity. Of course neural patterns as structures are as open to inheritance as are bone structures. And the widespread existence in animals below man of essentially stereotyped unlearned responses is enough to satisfy many students of the reality of inherited neural patterns. Nevertheless, the situation would be very much more satisfying if it were possible to point to genetic results where the inherited behavior patterns could not be due to receptor, effector, or other non-neural structure differences. Two illustrations will help make clear the kind of data that I hope some one will secure. Most birds appear to have the sensory and motor equipment for nest building, but not all of these birds build nests nor, where they do, do they build nests of equal complexity. Since the behavior runs true to the variety of bird, since it is not due to imitation of the parents and has no learning history in the individual's lifetime, it is surely an instinct, a behavior pattern fundamentally controlled by inherited neural connections. By contrast we may consider the voice of the mule which is more like that of the ass than that of the horse. This difference may be due to inherited vocal structures rather than to inherited neural patterns which control what the vocal structures do.

It is man's lack of elaborate, unlearned stereotyped forms of externally observable behavior which has led to the denial of the importance of heredity in human behavior and which has led specifically to the denial of human instincts. If man periodically manifested an elaborate unlearned courtship and mating ritual, if the human female came into heat at stated intervals and then performed a fairly fixed pattern of behavior, if man did not need to learn to build houses and yet did build them periodically and always essentially to the same plan, then there would only be a few recalcitrant souls to deny the direct role of heredity in determining human behavior. However, the evolutionary development which culminated in the primates did not proceed by merely continuing the type of behavioral organization found in lower animals. To have done so would have meant primate dominance by insect-like instinctive behavior with a relative neglect of learning, symbolic processes, and other plastic modes of adjustment. In the primates there is not only a marked cephalization in the organization of neural and behavioral controls; there is also, as has been pointed out today, a partial independence of external behavior from hormonal control. Thus, I may say, as McDougall recognized, evolutionary development has largely freed man from a dependence upon directly inherited behavior patterns except for those controlling reflex responses, emotions, drives, and certain general capacities.

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